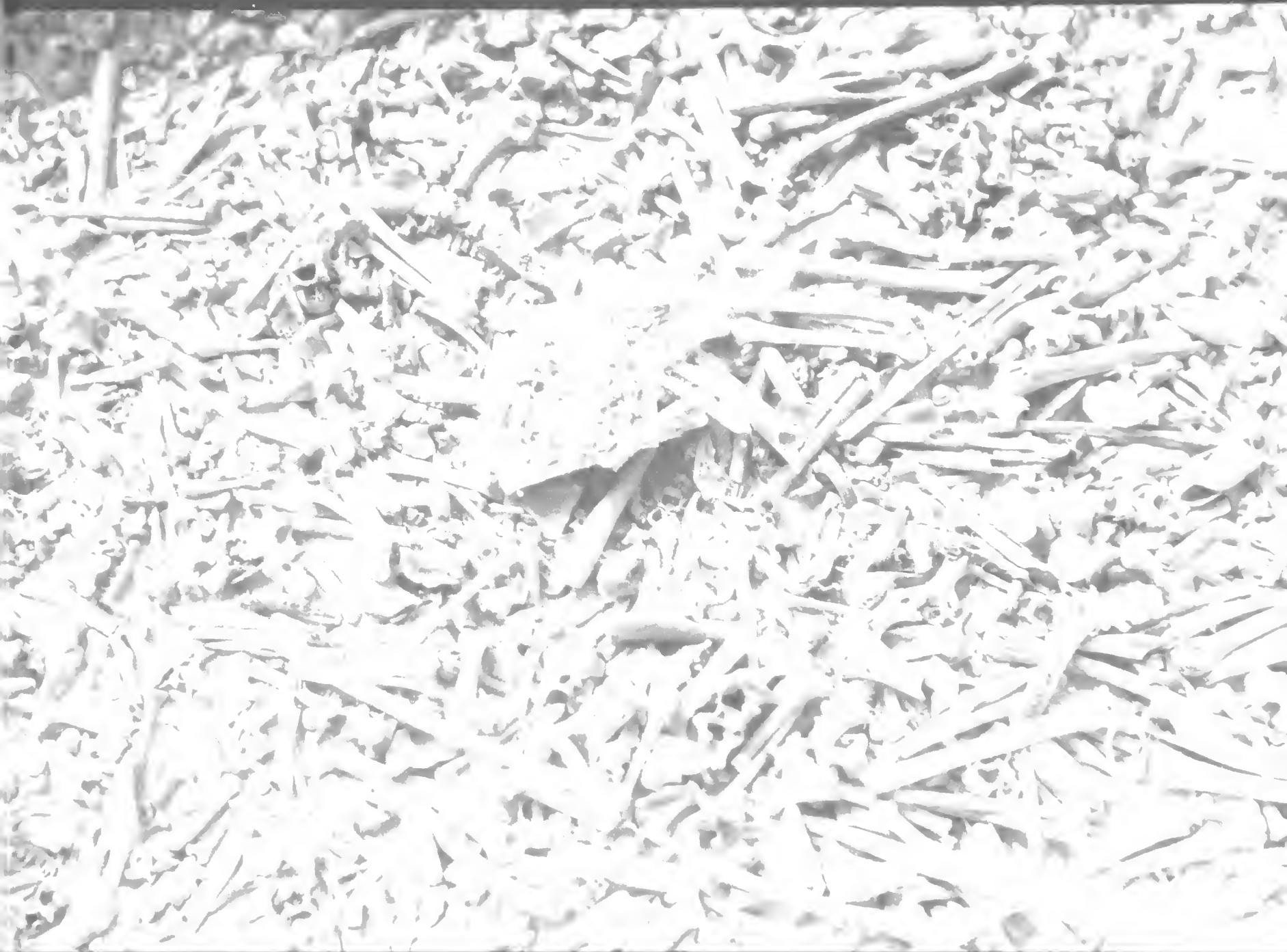


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LATE QUATERNARY VERTEBRATE FAUNAS OF THE LESSER ANTILLES: HISTORICAL COMPONENTS OF CARIBBEAN BIOGEOGRAPHY

GREGORY K. PREGILL, DAVID W. STEADMAN, AND DAVID R. WATTERS

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LESSER ANTILLES: HISTORICAL COMPONENTS OF
CARIBBEAN BIOGEOGRAPHY**

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ABSTRACT

The vertebrate fossil record of the Lesser Antilles, restricted to the late Quaternary, contains a wealth of biogeographical and systematic data on Caribbean amphibians, reptiles, birds, and mammals. Fifteen noncultural (paleontological) sites, known from seven islands, are both late Pleistocene and Holocene in age. New fossil material from seven of these sites is described herein. Thirty-three cultural (archaeological) sites, known from 16 islands, are mostly less than 2,000 years old (latest Holocene). The vertebrate record from the first two millennia of human occupation in the Lesser Antilles (ca. 4,000–2,000 years ago) is relatively poorly documented, but the record is sufficient for the following 1,500 years to reveal patterns of human subsistence and their

effect on indigenous populations of vertebrates. Noncultural, late Pleistocene vertebrates are best known from caves in the Leeward Islands, especially Barbuda. Practically all of the numerous extinct species or populations of iguanians, various birds, and bats from these sites in the Leeward Islands have Greater Antillean affinity. The faunal distinction between the Greater and Lesser Antilles that is evident today was almost nonexistent during the late Pleistocene at least as far south as the Guadeloupe Passage. The Holocene vertebrate record, whether from cultural or non-cultural sites, reveals 79 species and populations that no longer occur on a given island. Most, perhaps all, of these faunal losses can be related to prehistoric and/or historic human activities.

INTRODUCTION

The arc of islands comprising the Lesser Antilles (Fig. 1) is defined in the north by the Anegada Passage, the boundary with the Greater Antilles (Puerto Rico and the Virgin Islands, Hispaniola, Jamaica, Cuba), and in the south by the continental shelf of South America. From the most northerly island of Sombrero ($18^{\circ}30'N$) to the most southerly island of Grenada ($12^{\circ}N$), the arc stretches for 850 km and has a radius of curvature of about 450 km. The entire Lesser Antillean arc sits on the eastern margin of the Caribbean Plate, which is underthrust in a subduction zone by the crust of the Atlantic Plate (e.g., Bouysse, 1984; Westbrook, 1984; Maury et al., 1990).

The Lesser Antilles are usually described as a double arc, diverging north of Dominica into outer (eastern) and inner (western) chains. The islands of the outer arc (Marie Galante, Grande Terre [eastern] portion of Guadeloupe, La Desirade, Antigua, Barbuda, St. Barthelemy, St. Martin, Anguilla, Sombrero) are low-elevation compositions of older (mostly Eocene to Oligocene) volcanics variously overlain by carbonates, and therefore are sometimes referred to as the Limestone Caribbees (Martin-Kaye, 1959, 1969). The islands of the inner arc (Grenada, the Grenadines, St. Vincent, St. Lucia, Martinique, Dominica, Basse Terre [western] portion of Guadeloupe, Montserrat, Redonda, Nevis, St. Kitts, St. Eustatius, Saba) are composed mainly of volcanic rocks formed from the Miocene to the present, and are characterized by steep, mountainous terrain.

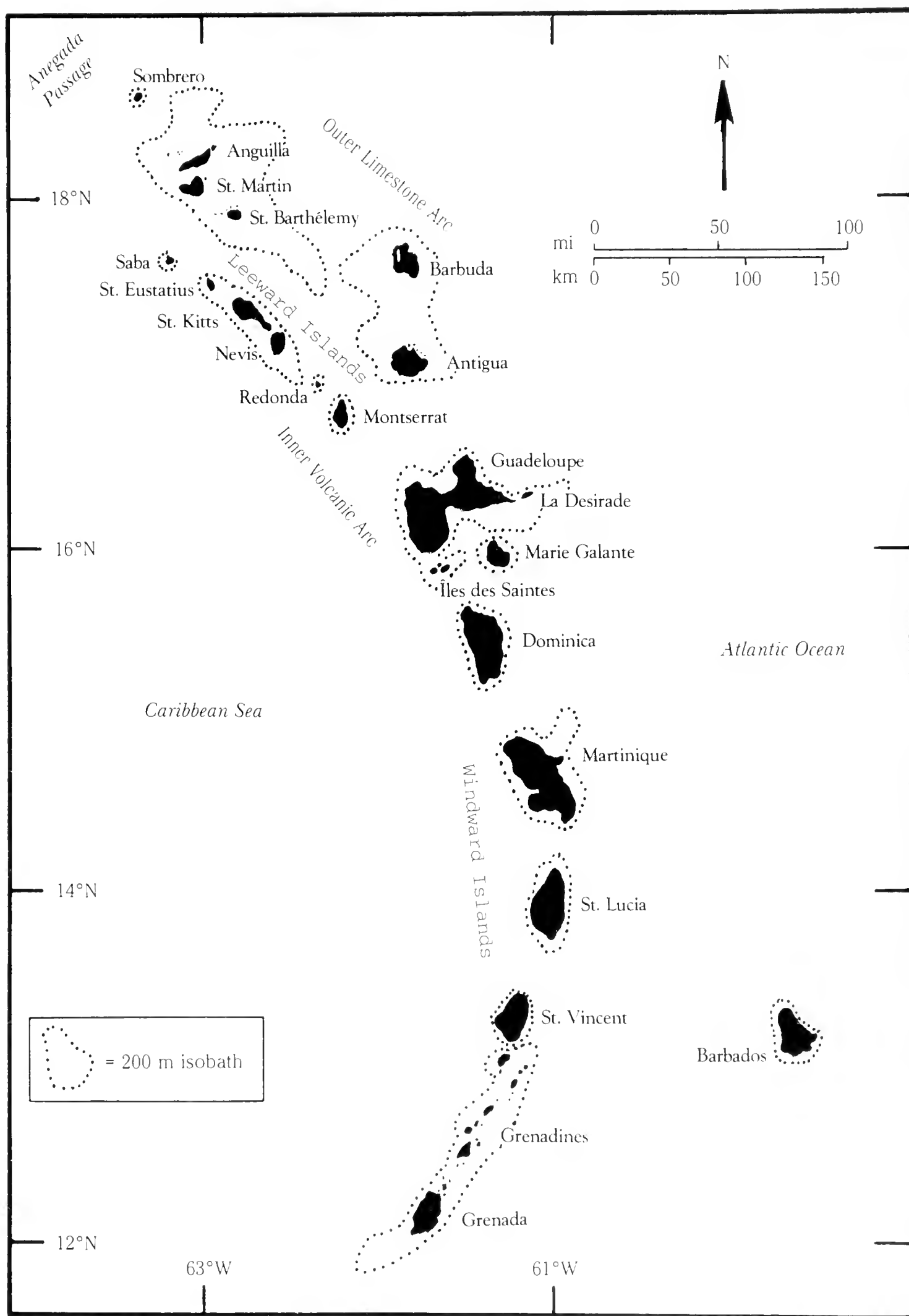
North of Guadeloupe, the inner and outer arcs constitute the Leeward Islands cartographically. From Guadeloupe south to Grenada the Lesser Antilles are referred to as the Windward Islands. Although not related tectonically to the inner or outer arc, Barbados, located about 175 km east of St. Vincent, is off the continental shelf and loosely associated faunistically with the Lesser Antilles. Trinidad and Tobago rest on the continental shelf of South America, possess a largely continental biota, and are not included in the Lesser Antilles. On some maps the Dutch islands of Aruba, Curaçao, and Bonaire are regarded as Lesser Antillean, but because their biota is distinctive we do not regard them as such.

None of the islands in the Lesser Antilles is particularly large. The total land area presently exposed

(about 6,600 km²) is less than that of Puerto Rico (8,897 km²). The land vertebrate fauna is related to, but not as rich in species as, the Greater Antilles. The fauna of the more southern islands of the Lesser Antilles shows less direct affinity with the Greater Antilles, and also shares species and genera with South America that do not reach the more northerly islands.

Because individual islands in the Lesser Antilles are less complex faunistically than those in the Greater Antilles, they have served as study sites for constructing and testing a variety of ecological models pertaining to species composition and colonization (e.g., Schoener and Gorman, 1968; Ricklefs and Cox, 1972, 1978; Williams, 1973; Terborgh et al., 1978; Roughgarden, 1983; Roughgarden and Pacala, 1989; Losos, 1992). Until recently, the fossil record was insufficient to test the historical reality of these models (Steadman et al., 1984a). Now the Holocene fossil record, while still far from complete, has revealed that the modern vertebrate fauna of the Lesser Antilles is not nearly as rich as it was several thousand years ago. On island after island, human activities of recent millennia have resulted in the loss of various indigenous rice rats, birds, lizards, snakes, and tortoises. Conversely, some species seem to have been transported from South America to the Lesser Antilles, as well as between islands, by Amerindians. Overall, the Lesser Antilles fauna has suffered as a consequence of human settlement and continues to be in decline (Westerman, 1952; Harris, 1965; Lescure, 1979; Steadman et al., 1984a; Pregill et al., 1988).

Fossil vertebrates are recovered from paleontological as well as archaeological contexts. Although fewer paleontological studies have been conducted in the Lesser Antilles than in the Greater Antilles, in both regions paleontological faunas derive at least in part from the remains of owl pellets deposited in limestone caves and sinkholes, and practically all date from the late Quaternary. In the Lesser Antilles, more vertebrate deposits have come from cultural (archaeological) sites than noncultural (paleontological) sites. Pre-Quaternary vertebrates have been found only on Grenada (Ronald Springer, personal communication, 1990); they are also rare in the Greater Antilles (e.g., Rieppel, 1980; Poiner and Cannatella, 1987; MacPhee and Wyss, 1990).



For the Greater Antilles, the most current overviews of the vertebrate fossil record are those of Pregill and Olson (1981), a treatment of West Indian fossil mammals by Morgan and Woods (1986), a checklist of fossil birds by Cuello (1988), and a review of Bahamian bats and rodents by Morgan (1989). No comprehensive summary exists for Lesser Antillean fossil vertebrates. The purpose of this paper is to fill that void. We will describe new specimens of fossil vertebrates from the islands of Anguilla, Barbuda, Antigua, and Guadeloupe, and summarize all other published occurrences of vertebrate fossils (excluding fish) from cultural and noncultural deposits in the Lesser Antilles. We restrict our summary to reports published through 1992, but add that vertebrate remains from archaeological sites on at least Anguilla, St. Martin, Saba, Nevis, and Montserrat are currently being studied by others.

METHODS AND TERMINOLOGY

Sources of Vertebrate Faunas

We use the term "fossil" to mean any bone from an archaeological (cultural) or paleontological (non-cultural) context, regardless of age or degree of mineralization. Appendix I is a species-by-island matrix of all late Quaternary records of amphibians, reptiles, birds, and mammals in the Lesser Antilles. Refer to Appendix I to associate common with scientific names used in the text. Table 1 lists all the localities from which the records derive. A detailed faunal summary for each island is provided as Appendix II.

The Lesser Antillean fossil record contrasts with that of the Greater Antilles in two important ways. First, whereas each of the four major Greater Antillean islands has extensive limestone formations with caves, most of the Lesser Antillean islands (at least for the inner arc) are composed of volcanic rocks, where dry caves or rockshelters are extremely scarce or absent. Thus, there has been little opportunity in the Lesser Antilles for long-term preservation of bones from owl pellets in caves. Second, most Lesser Antillean bone deposits are from archaeological sites—the "kitchen middens" of Amerindians usually deposited in calcarous beach sands or volcanic soils. Unfortunately, the late Quaternary faunas from both the Greater and Lesser Antilles suffer from a dearth of reliable chronologies based upon radiometric dating techniques.

As recently as 15 years ago, the entire prehistoric

record of Lesser Antillean birds consisted of a few bones each from Anguilla, St. Kitts, Antigua, Martinique, and Barbados (Olson, 1978). The records for amphibians, reptiles, and mammals were not much better. In 1980 GKP and DWS began a systematic search for fossil localities in the Lesser Antilles beginning with the most promising islands, the limestone group of the outer arc. By the end of 1990 we had surveyed many of the major islands of both the inner and outer arcs. In 1983 we (GKP, DWS, DRW) also began a fruitful interdisciplinary study of fossil vertebrates from selected archaeological contexts (Steadman et al., 1984b; Watters et al., 1984). The results of our field work followed initial predictions that few, if any, fossil vertebrates were to be found in noncultural contexts on the strictly volcanic islands, mainly because of an absence of suitable caves. On the limestone islands, however, late Quaternary sites have been located in caves, sinkholes, and rockshelters.

In Lesser Antillean archaeological sites the systematic recovery and recording of faunal remains began relatively recently. Prior to 20 years ago, archaeologists emphasized the recovery of ceramics and other artifacts for typological and chronological purposes. The faunal remains they encountered in sites were rarely retained or identified (e.g., Josselin de Jong, 1947; McKusick, 1960; Bullen and Bullen, 1972). Archaeological sediments now are routinely sieved through screens (usually $\frac{1}{4}$ " and/or $\frac{1}{8}$ " mesh), thereby greatly enhancing the recovery of faunal remains (Watters, 1989). Unfortunately, finer mesh screens ($< \frac{1}{8}$ "), which would retain the smallest bones, are used by archaeologists only in exceptional cases.

Regional Cultural Chronology

The initial colonization of the Lesser Antilles by Amerindian peoples, whose artifacts are classified within the Ortoiroid series, occurred by 2000 B.C. (and likely even earlier) in the Archaic Age of the regional chronology (Keegan and Diamond, 1987; Rouse, 1992) (Fig. 2). The coastal regions of north-east South America and the adjacent continental island of Trinidad are the areas from which the Ortoiroid peoples dispersed to the oceanic islands of the Lesser Antilles. In the Greater Antilles, a separate series (Casimiroid) is known from the Archaic Age and the even older Lithic Age (perhaps to 4000 B.C.). Although a Casimiroid population movement from the Greater Antilles into the northern Lesser Antilles during the Archaic Age remains

a possibility, such a colonization has yet to be verified archaeologically. It is the Ortoiroid artifact series from South America that characterizes the Archaic Age sites in the Lesser Antilles.

Lesser Antillean Archaic Age sites are usually coastal and often near mangrove stands (Davis, 1982). Faunal remains from these sites indicate that primarily marine and estuarine animals, especially mollusks, were exploited. These first inhabitants were neither agrarian nor potters—thus, the alternative cultural term “preceramic.” Archaic Age archaeological sites in the Lesser Antilles were recognized only within the past 20 years, and they are still minimally researched.

The Ceramic Age in the Lesser Antilles began about 500–400 B.C., with a northward migration of ceramic-producing Amerindians, represented by the Saladoid ceramic series, coming by way of Trinidad and the Orinoco drainage in South America. Ceramic Age sites are much more prevalent than Archaic Age sites, but again are primarily coastal. Evidence of exploitation of terrestrial as well as marine and estuarine faunas is found in these sites. Ceramic Age Amerindians were agriculturists. The earlier sites of the Ceramic Age (ca. 500 B.C.–A.D. 500; those with Saladoid ceramics) occur mainly but not exclusively on the volcanic islands of the Lesser Antilles, whereas later Ceramic Age sites (ca. A.D. 500–1500) are known from almost every island in both the limestone and volcanic arcs. Later Ceramic Age pottery in the Windward Islands is assigned to two ceramic series, Troumassoid and Suazoid (Fig. 2). Leeward Island pottery of the same time period is simply labelled as “post-Saladoid” ceramics.

The Historic Age began with European exploration (about A.D. 1500) and settlement (in the 1600s) of various Lesser Antillean islands. By the late 1700s most aboriginal peoples had been extirpated through warfare, disease, enslavement, and interbreeding, although remnant groups have persisted on a few islands even to the present.

Amerindian occupation in the Archaic and Ceramic ages is subsumed under the term “prehistoric” (= pre-Columbian) and is juxtaposed with the “historic” (= post-Columbian) occupation of Europeans and Africans. Prehistoric occupation of the Lesser Antilles spans at least 3,500 years whereas the historic occupation is 500 years old (Fig. 2).

The vertebrate faunas discussed below represent archaeological sites dating primarily to the Ceramic Age (ca. 500 B.C.–A.D. 1500). Little is known about vertebrates associated with the older (Archaic Age) or younger (Historic Age) sites.

Table 1.—*Late Quaternary vertebrate localities in the Lesser Antilles from north to south.*

| Island | Name of site | Context |
|---------------|-----------------------|----------------------|
| Sombrero | no name | noncultural |
| Anguilla | Apple Hole | noncultural |
| | Center Cave | noncultural |
| | Katouche Bay | noncultural |
| | Little Bay Cave | noncultural(?) |
| | The Fountain | cultural/noncultural |
| St. Martin | Cuckoo Hole | noncultural(?) |
| | Devel's [sic] Hole | noncultural(?) |
| | Hope Estate | cultural |
| Saba | Kelbey's Ridge | cultural |
| | The Bottom | cultural |
| St. Eustatius | Golden Rock | cultural |
| St. Kitts | Cayon | cultural |
| | Sugar Factory (Pier) | cultural |
| Nevis | Hichmans' Shell Heap | cultural |
| Antigua | Burma Quarry | cultural/noncultural |
| | Hawkes Bay | cultural |
| | Indian Creek | cultural |
| | Mill Reef | cultural |
| Barbuda | Barbuda I–V | noncultural |
| | Castle Bay Cave | noncultural |
| | Indiantown Trail | cultural |
| | Overview Cave | cultural |
| | Rat Pocket | noncultural |
| | Sufferers | cultural |
| | Two Foot Bay 1–3 | noncultural |
| Montserrat | Radio Antilles | cultural |
| | Trants | cultural |
| Guadeloupe | Morel à Moule | cultural |
| | Point du Capucin | noncultural |
| | Pointe de Vent | noncultural |
| Marie Galante | Folle Anse | cultural |
| | Talisronde | cultural |
| Martinique | Anse-Belleville | cultural |
| | Macabou | cultural |
| | Paquemar | cultural |
| St. Lucia | Grand Anse | cultural |
| Barbados | Chancery Lane | cultural |
| | Heywoods | cultural |
| | Hillcrest | cultural |
| | Ragged Point | noncultural |
| | Silver Sands | cultural |
| St. Vincent | Buccament Rockshelter | cultural |
| Grenadines | Mayreau Island Beach | cultural |
| Grenada | Calivigny Island | cultural |
| | Pearls | cultural |
| | Savanne Suazey | cultural |
| | Westerhall Point | cultural |

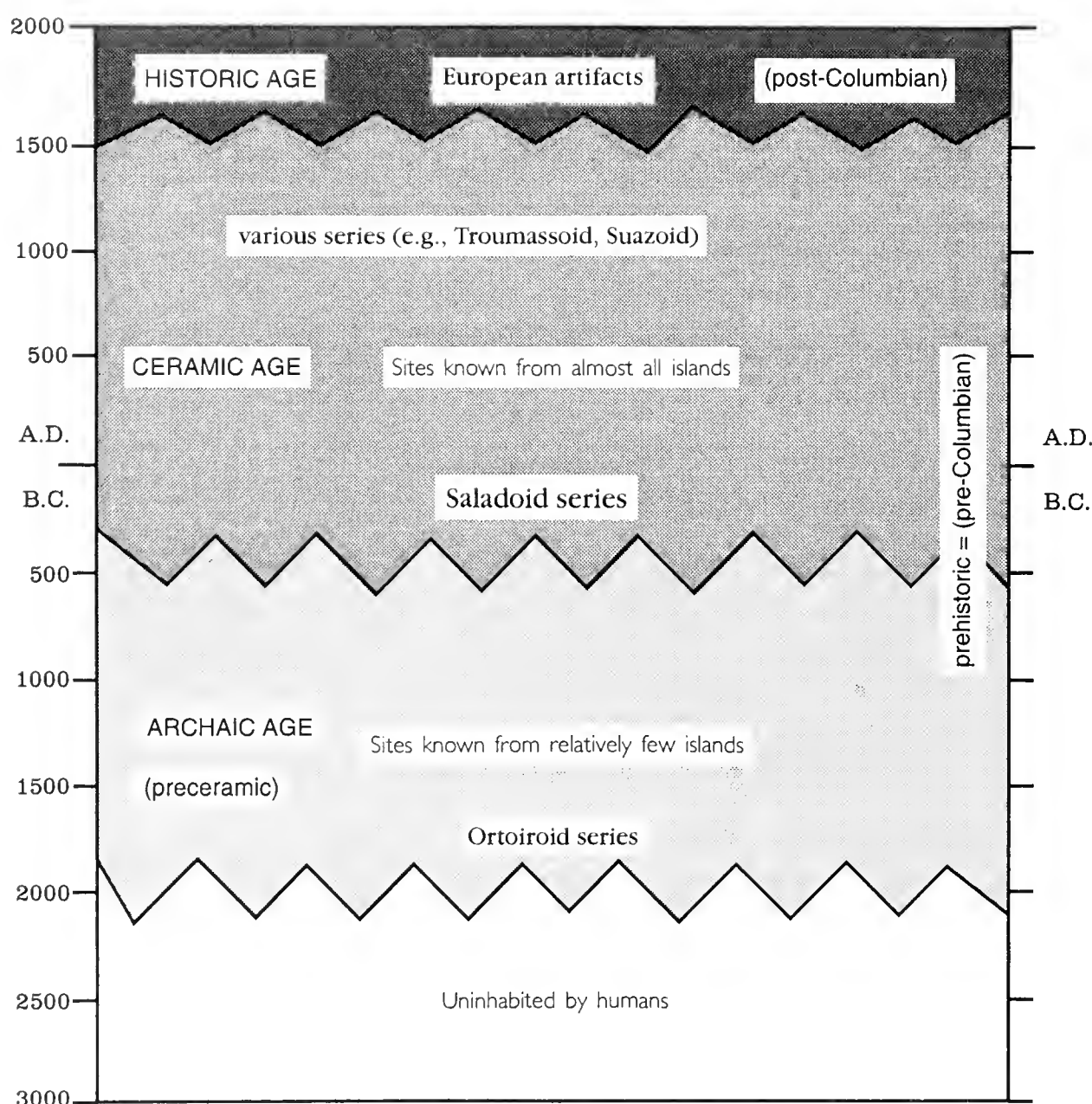


Fig. 2.—Cultural timetable of occupation by humans in the Lesser Antilles.

VERTEBRATE FOSSIL LOCALITIES IN THE LESSER ANTILLES

In this section, previously reported vertebrate faunas are summarized by island, listed from north to south (Table 1). However, for Anguilla, Barbuda, Antigua, and Guadeloupe new fossil data are presented separately in standard systematic order under each locality.

Fossil vertebrates have been reported in archaeological and paleontological contexts on various Lesser Antillean islands from Sombrero to Grenada. The occurrences are summarized below and in Appendices I and II. All of the cultural sites are entirely or partly prehistoric; that is, they date from Amerindian occupation ("pre-Columbian") prior to contact by Europeans, Asians, and Africans (the historic or "post-Columbian" period [Watters, 1989; and see above]). Usually the bones of vertebrates

from these aboriginal middens are found among abundant remains of mollusks and crustaceans that were taken for food (Fig. 3) (Watters and Rouse, 1989). In many published archaeological reports, bones often are referred only to class or genus, and in still other cases their identifications are questionable or unascertainable. Indeed, the basis of identification is rarely specified in most of these studies, nor is there an attempt to place terrestrial species and faunas in any distributional or zoogeographic framework, for example discriminating among indigenous species, introduced species, and those that were transported among islands by aboriginal people. Instead, the primary concern of zooarchaeology in the Lesser Antilles has been to interpret Amerindian subsistence patterns. In prehistoric aborigi-



Fig. 3.—Reliance on marine resources by Amerindians in the Lesser Antilles is evident in many archaeological sites. Shown here is a molluscan shell heap (*Cittarium pica* and *Strombus gigas*) from the Indiantown Trail site on Barbuda.

nal sites, fish generally are the dominant vertebrates in terms of both taxonomic diversity and in numbers of individuals. Our focus here is restricted to vertebrates other than fish.

No nonvolant native mammals currently inhabit the Lesser Antilles, although numerous species of rice rats and other rodents have become extinct recently, and nondomesticated species have been introduced (e.g., opossum, armadillo, agouti, monkeys). Taxonomic problems persist among some of these species, and has led to nomenclatural confusion in the zooarchaeological literature. For example, the agouti, *Dasyprocta* spp., was brought to the Lesser Antilles by the Amerindians, and has been referred to variously as *D. agouti*, *D. cristata*, or *D. leporina*. Equally unclear is whether more than one species is involved, as these taxa have been synonymized with each other in the past (Wilson and Reeder, 1993). Herein, we refer to the agouti simply as *Dasyprocta* sp. Similarly, the numerous cricetid rodents known only by fossils (*Oryzomyini* spp.), or

those that have become extinct historically (e.g., “*Megalomys*” from Martinique and St. Lucia), have yet to be reviewed systematically. For the most part we refer to all of these rice rats as *Oryzomyini* spp. following Steadman et al. (1984b).

SOMBRERO

Located 48 km northwest of Anguilla in the Anegada Passage, Sombrero is the northernmost of the Lesser Antilles and also one of the smallest (5.2 km²). It is a (now) flat (12 m elevation) limestone island that was uninhabited when mining of its extensive guano and phosphate deposits began in 1856. The mining operations leveled most of the island and uncovered the only vertebrate fossils known from Sombrero—an extinct tortoise (*Geochelone sombreroensis*). The type material described by Leidy (1868) as *Emys sombreroensis* is now lost, but consisted of the posterior portion of a plastron, a partial femur, and miscellaneous scraps. That taxon was placed in the synonymy of *Testudo* by Williams

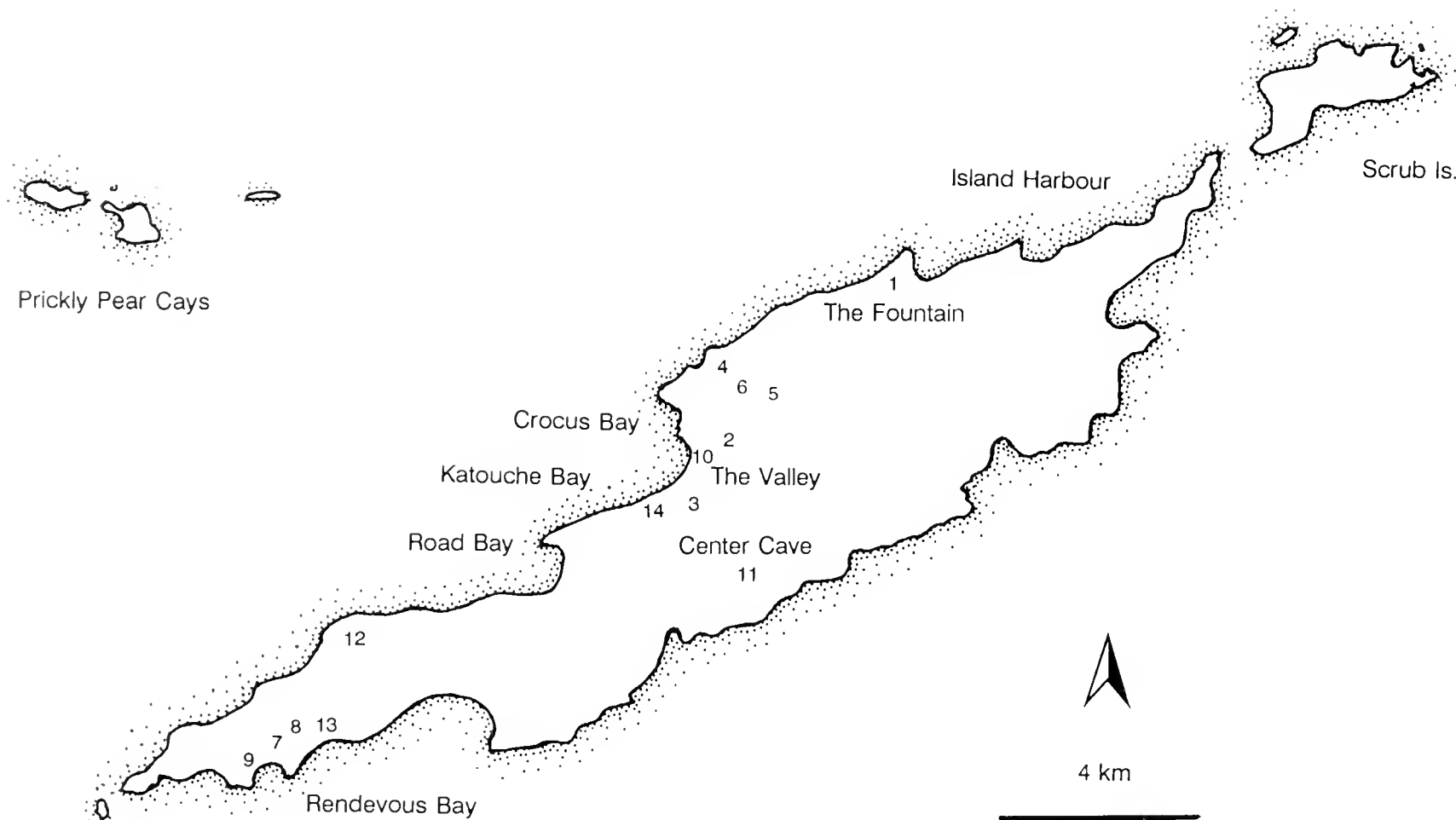


Fig. 4.—The island of Anguilla in the Leeward Islands. Numbered localities indicate the approximate location of late Quaternary vertebrate localities discussed in the text.

(1952), and subsequent material was obtained by Auffenberg (1967) who made comparisons with other fossils of *Geochelone* from the Greater Antilles. Unfortunately, none of the other fossil material of West Indian tortoises is particularly diagnostic, and the identity and phylogeny of the extinct West Indian forms remain poorly understood (Olson et al., 1990).

ANGUILLA

Anguilla (Fig. 4) is situated on a large submarine bank with the islands of St. Martin and St. Barthélemy. The bank is separated from the British Virgin Islands to the northwest by the Anegada Passage. To the south lie Saba and the islands of the St. Kitts Bank, and to the southeast are Barbuda and Antigua. As its name implies, Anguilla is long (26 km) and narrow (4.8 km at its widest point). It has an area of 90.5 km² and a maximum elevation of about 64 m above sea level. The north coast is generally quite steep, formed by high cliffs of 30 m or more (Fig. 5), whereas the south coast is a flat, rocky shore with scattered sandy beaches and coral reefs. Anguilla is composed almost entirely of Miocene limestones

resting on volcanics (Martin-Kaye, 1959). Solution features such as caves and sinkholes are common on this relatively arid island. The vegetation is dominated by thornscrub, most of which is second growth (Howard and Kellogg, 1987).

During 1–16 October 1982, GKP and DWS searched over 30 caves and other karstic features for vertebrate fossils. These features range from mere cliff overhangs to deep (>18 m), cavernous sinkholes. More than half of these caves, sinkholes, or shelters are known by local names:

1. The Fountain.—A large sinkhole a few hundred meters inland from Shoal Bay. Archaeological (Watters, 1991) and paleontological (reported herein) material present.
2. Apple Hole.—A large and very deep sinkhole located northeast of North Side Settlement. Requires ropes and ladders. The site is called Pitch Apple Hole by McFarlane and MacPhee (1989).
3. Cave at Katouche Bay.—A well-known, extensive tubular cavern near the head of Katouche Bay. Meandering and rocky without appreciable sediment; extensively mined for phosphate



Fig. 5.—The east ridge of Katouche Bay, north-central coast of Anguilla. Composed almost entirely of Miocene limestone, the island has little topographic relief but for the steep cliffs forming much of Anguilla's northern shoreline.

- in the past. Inhabited by at least two species of bats.
4. Isaac's Cave.—A cliff overhang on the coast northeast of North Side Settlement, 2 km east of Blackgarden Bay. Exposed seaward, rocky, little sediment.
 5. Sinkholes near Brimogen.—Six of these were investigated, but doubtless there are others in the area. Mostly small, rocky depressions with little sediment.
 6. John Lee Cave.—One of the many sinkholes in the vicinity of Brimogen. Used today as a shelter by wandering goats.
 - 7, 8. Rabbit's Hole and Dog Cave.—Rabbit's Hole and Dog Cave are adjacent rocky sinkholes near Cove Bay. Dog Cave is especially loathsome because of the voluminous garbage and numerous animal carcasses (thus the name) that litter the bottom of this present-day pet cemetery.
 9. Diana's Cave.—A small cave between Cove Bay and Cove Pond.
 10. Katouche Bay Parking Lot Cave.—A small cave on the hillside ridge overlooking Katouche Bay to the west, reached by following the road out of Crocus Hill. Shallow sediment containing a few scattered bones of lizards and birds.
 11. Center Cave.—A low, broad cave with a narrow surface-level entrance, on property of Mr. Gumbs, about 0.3 km northeast of airstrip. Rocky with considerable sediment, slightly damp. Vertebrate fossils recovered and reported herein.
 12. Sinkholes and cliff overhangs near Long Bay.—A series of shallow sinkholes and cliff overhangs north from Long Bay Village, none with apparent paleontological potential.
 13. Joseph's Hole.—A small sinkhole about 3 m deep located directly behind the Merrywing Hotel. Very little sediment.

14. Cliffs of Katouche Bay. — A series of large overhangs following the east ridge of Katouche Bay, best approached from North Hill Village.

As a fossil locality, Anguilla is famous for *Amblyrhiza inundata*, the extinct, giant rodent described by Cope (1869a, 1869b) from bones found in a block of phosphate sent to him in Philadelphia by a mining company. The exact locality from which Cope's holotypical material had been excavated was never specified. In 1922, ornithologist James L. Peters attempted to collect more specimens of *Amblyrhiza*, but found "... that the phosphate bed in which the type was found was completely exhausted ..." (Barbour, 1923:1). Additional remains of *Amblyrhiza* were reported by Cope (1883) and Ray (1964b), the latter based on material collected by H. E. Anthony in ca. 1926. McFarlane and MacPhee (1989) traced the history of the *Amblyrhiza* material studied by Cope and that collected by Anthony, determining that the collections of both Cope and Anthony included a few bones from St. Martin, but that the majority of specimens in each instance came from Anguilla. New specimens of *Amblyrhiza* were reported by Biknevicius et al. (1993).

A few fossils of bats from Anguilla are in the University of Florida Paleontology Collection. There are two dentaries of *Macrotus waterhousii* from Little Bay Cave, Anguilla, collected in 1958, as well as three dentaries (UF3376) of *Mormoops blainvillei* from "Cave I, Little Bay (surface)," collected by W. Auffenberg and W. King in July 1958. Neither of these Greater Antillean species presently occurs in the Lesser Antilles.

Although neither contained bones of *Amblyrhiza*, two sites that we found on Anguilla (Center Cave and The Fountain) yielded bones of various reptiles, birds, and mammals. According to the property owner, Center Cave (Fig. 6) is so named because it is located in the center of what was once a plantation. The cave entrance, at ground level, is a low slit approximately 3 m wide. The descent through a vertical passage leads into the south side of a wide, circular chamber. The ceiling is less than 2 m high in most places. Several blind passages radiate from the west and east walls. Humidity is high inside the cave. Most of the floor is covered with pebble- to boulder-sized limestone breakdown. The color (Munsell Soil Color Chart) of the poorly stratified, slightly organic sediment is 5YR 5/6 yellowish red (dry) and 2.5YR 3/6 dark red (wet). We screen-washed the sediment (a pebbly, sandy silt) from three

test pits (each 0.5 × 1.0 m). A radiocarbon age of 730 ± 60 years B.P. was obtained from a wood sample taken 10 cm below the surface of Test Pit 1 (University of Arizona Laboratory of Isotope Geochemistry No. A-3281). Aside from the reptile and bird bones described below, each of the test excavations yielded wood charcoal, terrestrial and marine mollusks, and bones of fish, bats, and introduced rodents (*Mus*, *Rattus*). There were also scraps of introduced ungulates, and many specimens of an undescribed, extinct species of oryzomyine rodent. No human artifacts were found.

The Fountain, located inland from Shoal Bay, is a large, deep, more or less circular sinkhole (Gurnee, 1989). It is the only exposed natural aquifer on the island. There are pools of water in the deepest recesses, and petroglyphs and scattered potsherds attest to its use by Amerindians. Interpreted as a late Ceramic Age ceremonial center, the archaeology of The Fountain is detailed by Watters (1991), who recovered and identified numerous corals and mollusks, and a single bone each of a teiid lizard (*Ameiva*), a possible stilt (*Himantopus himantopus*), and an unidentified mammal.

An iron ladder was installed during the 1950s to allow descent into The Fountain from the surface. Fossil-bearing sediment is scattered among unstratified, irregularly shaped deposits between limestone boulders. We excavated and dry screened a small pocket (1 × 1 m) of dry, powdery sediment (slightly pebbly, slightly sandy silt; 7.5YR 6/3 light brown dry) against the partial wall immediately west of the ladder. Aside from the bones of reptiles and birds described below, we recovered small pieces of wood charcoal (undated), terrestrial and marine mollusks, urchin spines, six fish bones, approximately 100 bat bones (unstudied), and many more specimens of the undescribed, extinct species of oryzomyine rodent.

Reptiles

Center Cave and The Fountain yielded a fairly rich assemblage of fossil lizards and snakes. The modern herpetofauna of Anguilla lacks native frogs, although *Eleutherodactylus johnstonei* has become established (GKP, personal observation; Censky, 1989). There are nine species of lizards (*Ameiva plei*, *Anolis gingivinus*, *Anolis wattsi pogus* [presumably extinct], *Hemidactylus mabouia*, *Iguana delicatissima*, *Mabuya "sloanei"*, *Sphaerodactylus macrolepis parvus*, *Sphaerodactylus sputator*, and *Thecadactylus rapicauda*), and one snake (*Alsophis rijersmai*). Fossils of at least five of these species



Fig. 6.—Most noncultural (paleontological) vertebrate fossils from the Lesser Antilles derive from the remains of owl pellets deposited in caves. On Anguilla, Center Cave (top) yielded a small, noncultural vertebrate fauna that is described in the text. Caves are a result of solution features in limestone, as in the cliffs and headlands along the east coast of Barbuda at Two Foot Bay (bottom). The caves in this area have yielded some of the earliest known and most abundant late Quaternary vertebrate faunas in the Lesser Antilles.

were found in addition to an extinct lizard of the genus *Leiocephalus*, previously unknown from Anguilla.

Thecadactylus rapicauda

Center Cave.—19 dentaries and fragments, 3 coronoids, 8 maxillae and fragments, 2 articular + surangular, 1 frontal, 1 parietal fragment, 1 pterygoid, 2 pelves. MNI (minimum number of individuals; following Pregill, 1981) = 13.

The Fountain.—13 dentaries and fragments, 20 maxillae and fragments, 1 premaxilla, 9 frontals, 3 partial parietals, 1 basioccipital, 5 pterygoids, 3 thoracic vertebrae. MNI = 10.

Dentaries of *Thecadactylus rapicauda* are distinguishable from those of the only other large West Indian geckos *Tarentola* and *Aristelliger* by their straighter teeth (Pregill, 1982). Elsewhere, *T. rapicauda* has been reported as a fossil from Antigua and Barbuda (Pregill et al., 1988).

The species occurs throughout the Leeward Islands and north to Necker Island in the British Virgin Islands, but had not been known from Anguilla prior to our field work. We collected *T. rapicauda* alive at two localities: at night on the wall of a work shed 0.5 km south of South Hill Village (USNM 236265–6), and 1.5 km northeast of North Hill Village in the twilight zone of the cave at the head of Katouche Bay (SDSNH 63991).

Sphaerodactylus sp.

Center Cave.—2 dentaries, 1 frontal. MNI = 1.

The dentaries of this small, leaf-litter gecko came from an individual(s) with an estimated snout–vent length (svl) of 30 mm. There are two species of *Sphaerodactylus* on Anguilla: *S. sputator*, which also occurs on St. Martin, St. Barthélemy, the St. Kitts Bank, and Sombrero, and *S. macrolepis*, a Greater Puerto Rican species known also from St. Martin, St. Barthelemy, and Dog Island.

Anolis spp.

Center Cave.—79 dentaries, 33 maxillae, 7 articular + surangulars, 17 frontals, 2 parietals, 1 post-orbital, 7 pterygoids, 10 pelves. MNI = 40.

The Fountain.—54 dentaries, 8 maxillae, 1 articular + surangular, 12 frontals, 2 parietals, 1 basioccipital, 6 pterygoids. MNI = 25.

Typical of many West Indian fossil sites derived from owl pellets, *Anolis* is the most abundantly represented vertebrate in both Center Cave and The

Fountain. Two species of *Anolis* are known historically from Anguilla, although one of these, *A. wattsi* (*pogus*), is now presumed to be extinct there (Lazell, 1972). The other, *A. gingivinus*, occurs island-wide on practically every shrub, bush, and tree trunk. Osteologically, there is little to separate these two species other than the larger size of *A. gingivinus*.

The dentaries of *Anolis* from both sites fall into two discrete size classes that correspond to the dimensions (svl) of modern *A. gingivinus* and *A. wattsi*. Tooth row lengths range from 8.7–10.2 mm in the larger series of dentaries, and from 6.2–7.9 mm in the smaller series. These two series represent individuals with estimated svls of 55–65 mm and 39–50 mm, respectively. On Anguilla, males of *A. gingivinus* have an average maximum svl of 60 mm. Male *Anolis wattsi pogus* from St. Martin have an average maximum svl of 50 mm.

Anolis wattsi pogus is known from Anguilla by two specimens (MCZ 16596–16597) supposedly collected in 1922 by J. L. Peters (Lazell, 1972). Today on Anguilla the humid, shady habitat in the vicinity of Katouche Bay appears comparable to areas on St. Martin where the same subspecies can still be found, although we and others (Lazell, 1972; Roughgarden and Pacala, 1989) failed to locate any surviving populations. *Anolis wattsi pogus* is more mesophyllic than other subspecies of *A. wattsi*, and there is little basis on which to judge its former range on Anguilla prior to the land being cleared in historic times. In any case, the area near Center Cave is presently barren pasture punctuated by clumps of scrub, a habitat wholly unsuited for this lizard.

Leiocephalus cf. *L. cuneus*

Center Cave.—1 left dentary. MNI = 1.

This single fossil dentary was referred to *Leiocephalus* by Pregill (1992) on the basis of several diagnostic features. However, it could be assigned only tentatively to species: *L. cuneus*, a fossil species which is known from the Antigua Bank (Etheridge, 1964; Watters et al., 1984; Pregill et al., 1988). Additional fossils of cf. *L. cuneus* were reported from Anguilla by Roughgarden and Pacala (1989). Still others, collected from Grand Terre, Guadeloupe, may also belong to *L. cuneus* (Pregill, 1992, and see below).

Ameiva plei

Center Cave.—8 dentaries and fragments; 3 maxillae; 2 articular + surangulars; 71 thoracic vertebrae; 2 pelves. MNI = 5.

The Fountain.—6 dentaries; 8 maxillae; 1 premaxilla; 2 articular + surangulars; 1 quadrate; 4 prefrontals; 3 frontals; 2 pterygoids; 2 scapulocoracoids; 1 thoracic vertebra; 1 ilium. MNI = 4.

The largest fossils came from individuals with svl approaching 120 mm. The smallest had a svl of approximately 50 mm. *Ameiva plei*, endemic to the Anguilla Bank, is a common resident of the island. The highest population density that we encountered on mainland Anguilla was in the thick, shady woods at the mouth of Katouche Bay. As with most species of *Ameiva*, *A. plei* is a wary animal. Curiously, the melanistic population (*A. corax*, Censky and Paulson, 1992), which is isolated on Little Scrub Cay off the northeast coast of Anguilla, is utterly without fear of humans. Clusters of 20 or more individuals would scavenge on fish remains at our feet, some having the temerity to climb on our boots and pant legs to get at the scraps of food we tossed their way. Perhaps this extreme tameness, reminiscent of lava lizards (*Tropidurus* spp.) in the Galápagos Islands, is a function of the lack of introduced predators on Little Scrub Cay (see Steadman, 1986).

Alsophis rijersmai

Center Cave.—1 partial dentary; 70 vertebrae. MNI = 1.

The Fountain.—12 vertebrae. MNI = 1.

Most of the fossil bones are comparable in size to those of a female of this species we collected 1 km west of Savannah Bay, Anguilla (SDSNH 63617, svl 458 mm).

Like *Ameiva plei*, *Alsophis rijersmai* is endemic to the Anguilla Bank. Both probably persist on Anguilla because the mongoose is absent. It has not been reported previously as a fossil.

Birds

Puffinus lherminieri

Center Cave.—1 tibiotarsus. MNI = 1.

The Fountain.—1 quadrate, 2 pedal phalanges. MNI = 1.

These bones represent the first record of *P. lherminieri* from Anguilla. This shearwater is common in paleontological and archaeological sites on Antigua and Barbuda. Very few nesting localities remain in the Lesser Antilles for this once widespread species.

Falco sparverius

Center Cave.—13 bones. MNI = 1.

This small falcon is common today on Anguilla and throughout the northern Lesser Antilles.

Zenaida aurita

Center Cave.—1 femur. MNI = 1.

This is one of the most common and widespread columbids on Anguilla and throughout much of the West Indies.

Columbina passerina

Center Cave.—1 mandible, 1 dentary. MNI = 1.

The status of *C. passerina* is similar to that of *Zenaida aurita*.

Margarops fuscatus

Center Cave.—1 quadrate, 1 rostrum. MNI = 2.

The Fountain.—1 adult tibiotarsus, 57 juvenile bones. MNI = 2.

This thrasher is fairly common in wooded parts of Anguilla today.

Tiaris bicolor

Center Cave.—1 mandible, 1 tibiotarsus, 1 tarsometatarsus. MNI = 1.

This tiny grassquit is locally abundant on Anguilla today.

Each of these five species of landbirds tolerates disturbed, cleared habitat. The absence from the Anguilla deposits of such forest-indicator taxa as Quail-Dove (*Geotrygon* sp.), Trembler (*Cincloerithia* sp.), or Forest Thrush (*Cichlerminia* sp.) would suggest that little if any undisturbed forest occurred near these sites in late prehistoric or early historic times.

ST. MARTIN AND ST. BARTHÉLEMY

The earliest published accounts of vertebrate fossils from either of these two islands on the Anguilla Bank are references to *Amblyrhiza* by Cope (1869b), Molengraaf (1888), Rutten (1931), and Schreuder (1933). An American Museum of Natural History (AMNH) expedition to Anguilla and St. Martin by H. E. Anthony and George Goodwin in 1926 recovered further remains of this giant rodent on both islands, but, as with the type series, most of their material was found on Anguilla. Anthony and Goodwin's discoveries have been brought to light recently by McFarlane and MacPhee (1989).

In the AMNH, GKP found a few bones of an iguanid lizard, probably *Iguana*, that apparently were among the vertebrate fossils that Anthony and

Goodwin excavated on St. Martin. The fossils were accompanied by a hand-written label that read: "AMNH, 1927. Lizard. Cuckoo Hole, Simpson's Bay, St. Martins [sic] Anthony and Goodwin." They include a partial right scapulocoracoid, partial right pelvis, thoracic vertebra, and a few phalangeal elements. *Iguana delicatissima* is known historically from the island. In the University of Florida Vertebrate Paleontology Collection is a dentary of *Macrotus waterhousei* from "Devel's Hole, St. Martins" [sic] catalogued as UF 3297. There is no further information with the specimen.

Recent archaeological excavations at the Hope Estate site, French St. Martin, uncovered a concentration of bone fragments identified as "*Oryzomys* [sic] sp. and also pigeons, doves and one snake cf. *Alsophis*" (Haviser, 1991:649). The identifications were made by E. S. Wing, who also noted that at 30% the MNI for terrestrial vertebrates was unusually high relative to fish and crabs. No complete faunal list was included in this preliminary report (Haviser, 1991). Artifacts indicate an early Ceramic Age (ca. 500 B.C.) occupation of the Hope Estate site.

We briefly surveyed the small island of St. Barthélemy on 17–20 October 1982. It is steep, rocky (volcanics) and densely populated. Several recesses and overhangs with possible paleontological potential were identified, but they were situated high up on nearly vertical, inaccessible cliffs. St. Barthélemy has received little attention archaeologically.

SABA

Approximately 50 km south of St. Martin is the small (ca. 13 km²) island of Saba, a Pleistocene volcano rising steeply from the ocean floor. The few faunal remains known thus far are from sporadic archaeological work that began in the early 1920s at The Bottom (Josselin de Jong, 1947). A summary of sites was provided by Haviser (1985). There have been recent excavations of a site at Spring Bay with an estimated age of A.D. 650–1350, and at Kelbey's Ridge, which is a late occupation site dating to about A.D. 1300–1450 (Hofman and Hoogland, 1991).

Josselin de Jong (1947:5) made passing mention of "birds' and fish-bones . . . and bone fragments" from his excavations at The Bottom. The preliminary observations of the faunal remains from Kelbey's Ridge note "the total absence of crabclaws among the food remains" and that "skeletal remains of birds could only be found in very small amounts or were not present at all, whereas large amounts of

Boobie (*Sula* sp.) remains were found in one of the Spring Bay sites" (Hofman and Hoogland, 1991:481).

ST. KITTS BANK

This locality includes St. Kitts, St. Eustatius, and Nevis. Vertebrate faunas are known from archaeological sites on each of these islands. St. Kitts (St. Christopher) lies 64 km west-northwest of Antigua. St. Eustatius lies 11 km north of St. Kitts, whereas Nevis, to the south, is separated from St. Kitts only by a shallow (4–5 fathoms), 3 km-wide channel. St. Kitts, the largest of the three, is approximately 30 km long and 10 km wide (176 km²), and consists of three connected mountain peaks with a maximum elevation of 1,307 m. The rocks are mostly andesitic volcanics dating from the Miocene through the Quaternary (Martin-Kaye, 1959).

St. Kitts has received considerable attention from archaeologists since the beginning of this century (Branch, 1907; summarized by Goodwin, 1979). The earliest mention of fossil vertebrates is Branch's (1907:332) passing comment on a midden that was exposed by a road cut near Stone-fort: "... fish-bones, bones of birds and a small mammal are extremely plentiful." The first actual faunal lists were produced in the companion studies of Hoffman (1973) and Wing (1973) who reported vertebrates from Amerindian middens at the Sugar Factory archaeological site near Basseterre south of Rawlins Bay, St. Kitts. This site was estimated to have been occupied from A.D. 700–1000. The remains include 15 species of fish, an indeterminate number of sea turtles (Cheloniidae), two squamate reptiles (the lizard *Iguana* sp., and the ground snake *Alsophis* sp.), two birds (*Porphyryla martinica*, and an unidentified species), and four mammals (manatee, pig, agouti, and rice rat). Steadman et al. (1984b) discussed the occurrences of rice rats from this and other Lesser Antillean archaeological sites.

Additional midden remains reported by Wing and Scudder (1980) were excavated from the Sugar Factory Pier and Cayon archaeological sites. This study did not mention the relationship between Sugar Factory Pier and the Sugar Factory locality of Wing (1973) and Hoffman (1973), but according to Goodwin (personal communication, 1993) they are components of the same large site. The Cayon site, on the other hand, is located 1.25 km inland from the east coast of St. Kitts overlooking the Cayon River. Of the two, the Sugar Factory Pier fauna is much larger, consisting of nearly 12,000 bones and frag-

ments. Thirty-six species of fish were identified. Lizards were represented by *Anolis* sp., *Iguana* sp., *I. delicatissima*, and *Ameiva* sp. On the St. Kitts Bank, *Iguana delicatissima* occurs on St. Eustatius, where the population is moderately abundant locally, and on Nevis it is known by one specimen (Lazell, 1973). None has been taken on St. Kitts proper, although the species undoubtedly occurred there in the past. Presumably, Wing and Scudder's (1980) referral of some of the iguana remains to *I. delicatissima* was based on geography; there is no discussion why some but not all iguana remains were so referred. Other reptiles in the midden fauna include the snake *Alsophis* cf. *rufiventris*, and sea turtle Cheloniidae sp. The bird bones were identified as *Sula* sp., *Nyctanassa violacea*, Rallidae sp. (unidentified rail), *Larus* sp., *Columba* sp., Turdidae sp. (unidentified thrush), and Icteridae sp. (unidentified oriole). The biogeographic significance of the birds would depend upon more refined identifications. The mammals consisted of rice rat, agouti, and dog, of which only the rice rat is indigenous. Rice rats and the ameiva were the most abundantly represented terrestrial species.

The faunal list provided by Wing and Scudder (1980) combined the results from both sites; hence some of these species might also have been found in the Cayon site, for which the only vertebrates mentioned specifically were dog, rice rat, and pigeon.

In February 1982, R. I. Crombie and DWS searched unsuccessfully for noncultural fossil sites on St. Kitts. The ornithological results of this trip have been summarized by Norton et al. (in preparation).

On St. Eustatius an early report by Josselin de Jong (1947) first brought attention to the Golden Rock archaeological site, where further excavations were conducted from 1984 until 1987 (Versteeg, 1991; Versteeg and Schinkel, 1992). Golden Rock yielded a rich vertebrate assemblage discussed and tabulated by van der Klift (1992). Sixty-two species were recorded, and of these, approximately 60% were fish. Remains of reptiles were identified as *Eretmochelys imbricata* (represented by a nearly complete skeleton), *Iguana* sp., *Iguana delicatissima*, *Anolis* sp., *Ameiva* cf. *erythrocephala*, unidentified Gekkonidae, and *Alsophis* cf. *rufiventris*. So far as identified, these taxa reside today on St. Eustatius.

Eighty bird bones from Golden Rock were referred to 17 genera or species and two indeterminate taxa, among which *Phoenicopiterus ruber* and *Athene cunicularia* are extirpated.

Seven mammals were listed from Golden Rock as Chiroptera sp., *Homo sapiens*, *Oryzomys* sp., *Dasyprocta aguti*, *Canis familiaris*, *Monachus tropicalis*, and Cetacea sp. Of these, specimens of the extinct rice rat "*Oryzomys* sp." were most abundant in the sample, and presumed to represent a single species (van der Klift, 1992).

The 132 km² island of Nevis has been the subject of a recent survey of settlement patterns, during which 21 archaeological sites were identified as spanning the last millennium B.C. to the historic period (Wilson, 1989). Of the test excavations undertaken, the Archaic Age sites of Hichmans' Shell Heap and Nisbetts produced faunal remains consisting of "coastal scatters of mollusks, land crab shells, fish bones . . ." and "sea turtle remains" (Wilson, 1989:427). No other faunal remains have been reported from Nevis.

ANTIGUA AND BARBUDA

Antigua and Barbuda share the same submerged bank in the Leeward Islands east of St. Kitts. Together, Antigua and Barbuda formed a single, much larger island during the lowered sea levels of Quaternary glacial intervals (Nicholson, 1976; Watters et al., 1992). Both of these islands have yielded important archaeological and paleontological faunas.

Antigua is a roughly triangular (280 km²) island composed of middle Tertiary and younger limestones in the north and east, and weathered middle Tertiary volcanics in the south. In between is a central plain consisting of late Tertiary sedimentary rocks derived from erosion of volcanics. The vegetation is a mixture of disturbed thorn scrub, agriculture, and semideciduous forest.

Vertebrate fossil localities on Antigua have been reviewed by Steadman et al. (1984a) and Pregill et al. (1988), who described the late Holocene fauna from the only known primarily noncultural site on the island, Burma Quarry in St. George Parish. The Burma Quarry site is a fossil-rich fissure developed in the limestone of north-central Antigua. Its significance lies in the high level of extinction among the species represented in the faunal assemblage, which dates to the early (Archaic Age) human settlement of the island (Steadman et al., 1984a; Pregill et al., 1988). Burma Quarry was the first West Indian vertebrate fauna of late Holocene age that clearly implicated human impact as a major cause of vertebrate extinction and extirpation on Caribbean islands. The occurrence of extinct and living species

Table 2.—Summary distribution of fossil vertebrates at Burma Quarry, Antigua, based upon data from Steadman et al. (1984a) and Pregill et al. (1988). The first number is for living species represented; the second number for species extinct on Antigua. Radiocarbon dates (years B.P.) on wood charcoal are: upper vertical unit, $2,560 \pm 70$; east and west horizontal units, $3,330 \pm 50$, $3,515 \pm 60$, $3,695 \pm 100$; lower vertical unit, $4,300 \pm 150$. NISP = number of identified specimens. Species are identified in Table 3 and Appendices I and II.

| | Upper vertical unit | East and west horizontal unit | Lower vertical unit | Tailings | Total |
|---------------|---------------------|-------------------------------|---------------------|----------|-------|
| Amphibians | 0/0 | 1/0 | 0/0 | 1/0 | 1/0 |
| Reptiles | 2/1 | 4/2 | 4/3 | 4/2 | 4/3 |
| Birds | 0/1 | 2/1 | 3/3 | 7/2 | 7/4 |
| Mammals | 1/1 | 3/2 | 4/4 | 5/2 | 4/5 |
| Total species | 3/3 | 10/5 | 11/10 | 17/6 | 16/12 |
| NISP | 21 | 227 | 156 | 365 | 769 |

from the Burma Quarry fissure is summarized in Table 2.

Elsewhere on Antigua there are important archaeological sites from which vertebrate remains have been recovered. The best studied of these are the Ceramic Age sites at Indian Creek (Fig. 7), Mill Reef, and Hawkes Bay (Wing et al., 1968; Olsen, 1974; Nicholson, 1983; Steadman et al., 1984a; Jones, 1985). The extirpated species found at these localities include the snake *Boa constrictor*, the birds *Puffinus lherminieri*, *Phoenicopterus ruber*, *Porphyryula martinica*, and *Amazona vittata*, and the mammals *Oryzomyini* new sp. and *Trichechus manatus*. Table 3 summarizes the extensive prehistoric record of birds from Antigua. Only two species, the extirpated *Puffinus lherminieri* and the extant *Zenaida aurita*, occur in all three sites. Five of the 11 species (excluding Passeriformes sp.) from Burma Quarry are shared with Indian Creek and/or Mill Reef, which themselves share only four of their combined 24 species.

Barbuda, in contrast to its sister island, is composed entirely of limestones built from an uplifted reef complex (Brasier and Donahue, 1985; Watters et al., 1992). It lies 40 km north of Antigua, has an area of 156 km², and a maximum elevation of 42 m in the Highland limestone. Most of Barbuda is covered in scrub and deciduous forest, although there are extensive salt ponds, marshes, and swamps.

On the east coast of Barbuda at Two Foot Bay (Fig. 6) nine caves have yielded some of the earliest known and most abundant fossil faunas from the Lesser Antilles, although many thousands of bones

Table 3.—Birds from paleontological and archaeological sites on Antigua. Numbers are NISP (numbers of identified specimens). From data in Wing et al. (1968), Steadman et al. (1984a), Pregill et al. (1988), and herein. x = occurs, but number of bones unknown. e = extirpated on Antigua.

| | | | |
|--|----|----|----|
| <i>Puffinus lherminieri</i> (e) | 1 | 10 | x |
| <i>Puffinus</i> cf. <i>P. puffinus</i> (e) | — | — | x |
| <i>Phaethon lepturus</i> | — | — | x |
| <i>Phaethon aethereus</i> | — | 3 | — |
| <i>Sula</i> sp. | — | — | x |
| <i>Fregata magnificens</i> | — | — | x |
| <i>Ardeola striata</i> | — | 1 | — |
| <i>Egretta</i> sp. | — | 3 | — |
| <i>Nyctanassa violacea</i> | — | — | x |
| cf. <i>Nycticorax nycticorax</i> | — | — | x |
| <i>Phoenicopterus ruber</i> (e) | — | — | x |
| <i>Anas bahamensis</i> | — | 1 | — |
| <i>Buteo platypterus</i> | — | 1 | — |
| <i>Poliolimnas flaviventer</i> (e) | 1 | — | — |
| <i>Porphyryula martinica</i> (e) | — | 8 | x |
| <i>Calidris melanotos</i> | — | 1 | — |
| <i>Calidris</i> sp. | 3 | — | — |
| <i>Larus atricilla</i> | — | — | x |
| <i>Columba squamosa</i> | — | 13 | x |
| <i>Zenaida aurita</i> | 1 | 17 | x |
| <i>Columbina passerina</i> | 11 | 2 | — |
| <i>Geotrygon mystacea</i> | — | 12 | — |
| <i>Amazona vittata</i> (e) | — | 2 | — |
| <i>Athene cunicularia</i> (e) | 13 | — | x |
| <i>Chordeiles gundlachii</i> | — | 1 | — |
| <i>Orthorhynchus cristatus</i> | 1 | — | — |
| cf. <i>Tyrannus dominicensis</i> | 1 | — | — |
| <i>Margarops fuscatus</i> | 6 | 2 | — |
| <i>Cinclocerthia ruficauda</i> (e) | 1 | — | — |
| <i>Loxigilla noctis</i> | 1 | — | — |
| Passeriformes sp. | 27 | — | x |
| Total number of species | 12 | 15 | 14 |

from these localities remain unidentified. Various investigators from the University of Florida in the late 1950s and early 1960s, including Walter Auffenberg, Robert Allen, Wayne King, William Joseph, and Clayton Ray, excavated sites known as Barbuda (Caves) I through V. The reptile and amphibian bones from these excavations were studied by Auffenberg (1958), Etheridge (1964), Lynch (1966), and Pregill et al. (1988). Barbuda I through V all lack radiocarbon chronologies. Most probably date to the late Pleistocene although much of the Holocene may be represented in some. A priority for future paleontological research on Barbuda would be to establish an absolute chronology for some or all of these sites.

In January 1983, we (GKP, DWS, DRW) briefly excavated bone deposits from some of the numerous other caves in the vicinity of Two Foot Bay. These shallow, unstratified but very fossiliferous deposits are also undated. Rat Pocket is a small, seaward-facing cave that is 3.0 m long and 3.4 m wide, with a 1.5 m-wide entrance. Excavation 1 ($0.5 \times 0.3 \times 0.2$ deep) is 0.4 m within the cave and 0.4 m south of the center line. Excavation 2 (also $0.5 \times 0.3 \times 0.2$ m deep) is 1.8 m within the cave, along the center line. The bones from Rat Pocket, the richest site, are on average darker and more mineralized than those from Barbuda I or II, or the other sites that we sampled. Most of the thousands of bones from Rat Pocket are of the large extinct rice rat *Oryzomyini* sp., although bones of an extinct, large barn owl (*Tyto* new sp.) were also recovered (Steadman and Hilgartner, in preparation), along with a variety of amphibians, reptiles, birds, bats, and nonnative mammals.

Among our other sites (January 1983) Excavations 1–3 at Two Foot Bay were in small caves about 50–75 m from Rat Pocket. Excavation 1 yielded only five bones of the extinct oryzomyine rodent, eight to ten bones of bats, and five bones of birds. Excavation 2 at Two Foot Bay produced a few fragments of oryzomyine rodent, 15 bat bones, seven bones of a juvenile goat (*Capra hircus*, nonnative), a maxilla of the black rat (*Rattus* cf. *R. rattus*, nonnative), and seven bird bones.

Excavation 3 at Two Foot Bay yielded two bat bones, a cervical vertebra of the extinct oryzomyine rodent, two postcranial bones of *Rattus* sp., and three bird bones. Each of the identifiable 13 bird bones from Excavations 1–3 at Two Foot Bay belongs to an extinct or extirpated species, including the only specimens of *Corvus* new sp. (see below).

We conducted another small test excavation in 1983 at a cave overlooking Castle Bay, thereby named Castle Bay Cave. The specimens recovered are one fish vertebra, an unidentified bat humerus, 18 bones of the fish-eating bat *Noctilio leporinus*, seven bones of a goat (*Capra hircus*, nonnative), three bones of *Rattus* cf. *R. rattus*, and eight bird bones.

There are two extinct squamates from the non-cultural Barbudan cave deposits. One is the Curly-tailed Lizard, *Leiocephalus cuneus*, the bones of which were common in many deposits, and were also present in the remains screened from the Indiantown Trail archaeological site (Watters et al.,



Fig. 7.—Our 1983 field team on Antigua screened for vertebrate remains from tailings at Indian Creek, a well-known Amerindian site on the island. Desmond Nicholson (top left in white shirt) leads one of the particularly active local archaeological societies in the Leeward Island.

1984). The other extinct squamate is a large iguanid (svl ca. 400 mm) of uncertain affinity represented by a single braincase from Barbuda III. Etheridge (1964) left this specimen unassigned, but noted consistent similarities shared with the Galápagos land iguanas *Conolophis* spp. that were not observed in his comparative skeletons of the only other large West Indian iguanids *Iguana* and *Cyclura*. The Barbudan fossil was reexamined by de Queiroz (1987) with a larger suite of comparative material. He was unable to refer the fossil conclusively, although he reasoned that the proportions of the parabasisphenoid reported by Etheridge (1964) did in fact fall within the ranges of modern *Cyclura* and *Conolophis*. The same observation was made by Pregill (1981) in describing fossil *Cyclura* from Puerto Rico.

Also problematic are two snake vertebrae from

Table 4.—Birds from paleontological and archaeological sites on Barbuda. Identifications by DWS. Numbers are NISP (numbers of individual specimens). *e* = extirpated species; *E* = extinct species.

| | Barbuda | | | | Rat Pocket | Two Foot Bay | | | Castle Bay Cave | Indian-town Trail | Total bones/sites |
|---|---------|----|-----|-----|------------|--------------|---|---|-----------------|-------------------|-------------------|
| | I | II | III | V | | 1 | 2 | 3 | | | |
| <i>Puffinus lherminieri</i> (e) | 19 | 5 | 1 | — | 3 | 3 | 4 | 2 | 4 | 6 | 47/9 |
| <i>Neochen</i> cf. <i>N. jubata</i> (e) | — | — | — | — | — | 1 | 2 | — | 3 | — | 6/3 |
| <i>Falco sparverius</i> | 1 | — | 1 | 1 | 1 | — | — | — | — | — | 4/4 |
| <i>Falco columbarius</i> | — | — | — | — | — | — | — | — | 1 | — | 1/1 |
| <i>Rallus limicola</i> (e) | — | — | 1 | 1 | — | — | — | — | — | — | 2/2 |
| <i>Burhinus</i> cf. <i>B. bistratus</i> (e) | — | — | 1 | — | — | — | — | — | — | — | 1/1 |
| <i>Columba leucocephala</i> | — | — | — | — | — | — | — | — | — | 2 | 2/1 |
| <i>Columba squamosa</i> | 1 | — | 1 | 4 | — | — | — | — | — | — | 6/3 |
| <i>Zenaida aurita</i> | 3 | 1 | 3 | 10 | 3 | — | — | — | — | — | 20/5 |
| <i>Columbina passerina</i> | 4 | 1 | — | 13 | 1 | — | — | — | — | — | 19/4 |
| <i>Geotrygon mystacea</i> | 3 | — | — | 9 | — | — | — | — | — | 1 | 13/3 |
| <i>Aratinga</i> new sp. (E) | — | 1 | — | — | — | — | — | — | — | — | 1/1 |
| <i>Tyto</i> new sp. (E) | — | — | — | — | 7 | — | — | — | — | — | 7/1 |
| <i>Athene cunicularia</i> (e) | 26 | 1 | 5 | 47 | 4 | — | — | — | — | — | 83/5 |
| <i>Sericotes holosericeus</i> | 3 | — | — | — | — | — | — | — | — | — | 3/1 |
| <i>Orthorhynchus cristatus</i> | 13 | — | — | — | — | — | — | — | — | — | 13/1 |
| <i>Myiarchus</i> cf. <i>M. oberi</i> | 1 | — | — | — | — | — | — | — | — | — | 1/1 |
| <i>Hirundo pyrrhonota</i> (e) | — | — | — | 3 | — | — | — | — | — | — | 3/1 |
| <i>Corvus</i> new sp. (E) | — | — | — | — | — | — | 1 | — | — | — | 1/1 |
| <i>Mimus gundlachii</i> (e) | 2 | — | — | 1 | — | — | — | — | — | — | 3/2 |
| <i>Margarops fuscus</i> | 7 | — | — | 4 | 1 | — | — | — | — | — | 12/3 |
| <i>Margarops fuscatus</i> | 2 | 1 | 1 | 26 | 9 | — | — | — | — | — | 39/5 |
| <i>Cinclocerthia ruficauda</i> (e) | 7 | — | — | 2 | 2 | — | — | — | — | — | 11/3 |
| <i>Cichlerminia lherminieri</i> (e) | 1 | — | — | 1 | — | — | — | — | — | — | 2/2 |
| <i>Vireo altiloquus</i> | — | — | — | 1 | — | — | — | — | — | — | 1/1 |
| <i>Loxigilla portoricensis</i> cf. <i>grandis</i> (E) | 2 | — | — | — | — | — | — | — | — | — | 2/1 |
| <i>Loxigilla noctis</i> | 2 | — | — | — | — | — | — | — | — | — | 2/1 |
| <i>Tiaris bicolor</i> | 1 | — | — | 1 | — | — | — | — | — | — | 2/2 |
| <i>Ammodramus savannarum</i> (e) | — | — | — | 1 | — | — | — | — | — | — | 1/1 |
| Total bones | 98 | 10 | 14 | 125 | 31 | 4 | 7 | 2 | 8 | 9 | 308/10 |
| Total species | 18 | 6 | 8 | 16 | 9 | 2 | 3 | 1 | 3 | 3 | 29 |

Barbuda I that Auffenberg (1958) referred to *Pseudoboa* cf. *P. cloelia* (= *Clelia clelia*). Auffenberg (1958) troubled over his referral of the fossil vertebrae, but dismissed notions that they came from any known Antillean xenodontine (e.g., *Alsophis*). In the Lesser Antilles, *Clelia errabunda* (= *C. clelia*) occurs on Dominica and St. Lucia (Underwood, 1993), and *C. c. groomei* is restricted to Grenada. *Clelia clelia* otherwise ranges throughout Central America and northern South America (Peters and Orcjas-Miranda, 1970). Our own excavations in caves at Two Foot Bay uncovered numerous snake vertebrae, all of which could be assigned to *Alsophis*. Although *Alsophis* is not known from Barbuda historically, we assume that the vertebrae from the caves represent the same species that now is practically extinct on Antigua, *A. antillensis antiquae* (Lazell, 1967).

Table 4 summarizes the prehistoric avifaunas from the various Barbudan sites. In systematic order, we will highlight selected taxa. Among the extinct/extirpated species, *Puffinus lherminieri* is represented by the second largest number of bones, but occurs at the most sites. This seabird nests in burrows or rock crevices and thus is vulnerable to predation by humans or other nonnative predators.

The "Orinoco" Sheldgoose (*Neochen* cf. *N. jubata*) is represented by a cervical vertebra from Excavation 1, Two Foot Bay; a carpometacarpus and a pedal phalanx from Excavation 2, Two Foot Bay; and a manual phalanx, tibiotarsus, and pedal phalanx from Castle Bay Cave. These specimens cannot be distinguished clearly from bones of modern *N. jubata* of tropical South America. Brodkorb (1964) described a new species of *Neochen*, *N. barbadiana*, from cave deposits on Barbados of presumed Pleis-

tocene age. In light of the new specimens from Barbuda, reexamination of the Barbados material is needed. Nevertheless, the genus *Neochen* is confined to tropical South America today. In the late Quaternary, presumably in the late Pleistocene, it occurred in the Lesser Antilles at least as far north as Barbuda.

The Virginia Rail (*Rallus limicola*) is represented by a scapula from Barbuda III and a tarsometatarsus from Barbuda V. This mainland North American species has not been recorded before from the West Indies, although it could be expected to occur in the Lesser Antilles as a rare vagrant. Perhaps there was a resident population of *R. limicola*, or an osteologically similar species, on Barbuda in the late Pleistocene.

The Thick-knee (*Burhinus* cf. *B. bistriatus*) is represented by a tibiotarsus from Barbuda III. This bird of savannas and grasslands today lives locally in the mainland Neotropics (including Margarita Island off the coast of Venezuela) and, within the West Indies, only on Hispaniola. There are also late Quaternary records of this taxon from the Bahamas (Pregill and Olson, 1981; Olson and Hilgartner, 1982; Olson et al., 1990).

The very large extinct parakeet *Aratinga* new sp. is represented by a distinctive left palatine from Barbuda II. It is larger than the palatine of any living species of *Aratinga* (Table 5), but is referred to *Aratinga* rather than *Ara* or *Amazona* (the other two indigenous genera of West Indian psittacids) based on the following: the distoventral surface is round and slightly expanded; in lateral aspect the proximal attachment deepens rapidly (relatively shallow in *Ara* and *Amazona*); and the medial articulation (with the paired palatine) is relatively small. In these three characters the Barbudan specimen also agrees with two other South American parakeets, *Cyanoliseus patagonicus* (Argentina) and especially *Ognorhynchus icterotis* (Colombia). In overall proportions (as determined by the ratio of distal width to ventral length; Table 5), the Barbudan specimen resembles allometrically the palatine of larger parakeets, whereas in species of *Ara* and especially *Amazona*, which are of similar lengths, the palatine is much more slender. Exclusive of the Caribbean Parakeet *Aratinga pertinax* from the islands off Venezuela, the modern species of *Aratinga* in the West Indies are the Hispaniolan Parakeet (*A. chloroptera*; Hispaniola, Puerto Rico, and Mona), the Cuban Parakeet (*A. euops*; Cuba, Isle of Pines), and the Olive-throated Parakeet (*A. astec*; Jamaica, Mexico, Central Amer-

Table 5.—Measurements (mm) of the palatine in various species of Neotropical parrots.

| | Ventral length (vl) | Distal width (dw) | dw/vl |
|-----------------------------------|---------------------|-------------------|-------|
| <i>Aratinga</i> new sp. (Barbuda) | 30.0 | 2.5 | .083 |
| <i>A. chloroptera</i> | 25.6 | 1.7 | .066 |
| <i>A. holochora</i> | 24.3 | 1.5 | .062 |
| <i>A. euops</i> | 18.9 | 1.3 | .069 |
| <i>A. astec nana</i> | 20.9 | 1.1 | .053 |
| <i>A. a. astec</i> | 18.4 | 1.0 | .054 |
| <i>A. canicularis</i> | 18.5 | 1.0 | .054 |
| <i>A. pertinax</i> | 19.2 | 0.7 | .036 |
| <i>Cyanoliseus patagonicus</i> | 26.6 | 1.5 | .056 |
| <i>Ognorhynchus icterotis</i> | 35.8 | 2.6 | .073 |
| <i>Ara macao</i> | 49.7 | 2.3 | .046 |
| <i>A. militaris</i> | 47.1 | 2.4 | .051 |
| <i>A. ambigua</i> | 54.0 | 2.3 | .042 |
| <i>A. arauna</i> | 47.7 | 1.7 | .036 |
| <i>A. nobilis</i> | 26.4 | 1.4 | .053 |
| <i>A. severa</i> | 32.2 | 1.4 | .044 |
| <i>Amazona farinosa</i> | 32.0 | 0.9 | .028 |
| <i>A. guildingii</i> | 31.0 | 1.2 | .039 |
| <i>A. arausiaca</i> | 30.4 | 1.0 | .033 |
| <i>A. imperialis</i> | 31.5 | 1.0 | .032 |
| <i>A. versicolor</i> | 28.7 | 1.0 | .035 |
| <i>A. vittata</i> | 22.1 | 0.6 | .027 |
| <i>A. ventralis</i> | 24.8 | 0.8 | .032 |
| <i>A. agilis</i> | 22.8 | 0.6 | .026 |
| <i>A. barbadensis</i> | 25.3 | 0.8 | .032 |
| <i>A. leucocephala</i> | 23.7 | 0.8 | .034 |

ica). Among these and mainland species of *Aratinga*, the Barbudan specimen is most similar to *A. chloroptera*.

The extinct large barn owl (*Tyto* new sp.) is represented by seven bones from Rat Pocket. All other extinct West Indian species of *Tyto* are from the Greater Antilles or the Bahamas. The Barbudan form appears most similar to *T. ostologa* Wetmore of Hispaniola. The only living species of *Tyto* in the West Indies are two relatively small species, *T. glaucops* of Hispaniola and the widespread *T. alba*.

The Burrowing Owl (*Athene cunicularia*) is represented on Barbuda at five sites and by more bones than any other extinct or extirpated species of bird. Today confined in the West Indies to the Greater Antilles and the Bahamas, *A. cunicularia* occurred until prehistoric or historic times on numerous islands in the Lesser Antilles (Pregill and Olson, 1981; Olson and Hilgartner, 1982; Steadman et al., 1984a; Pregill et al., 1988; Olson et al., 1990).

The Cliff Swallow (*Hirundo pyrrhonota*) is represented by two humeri and an ulna from Barbuda V. This species occurs in the West Indies today as an uncommon but widespread spring and autumn



Fig. 8.—Overview Cave on Barbuda is a “closed” or sheltered archaeological site (see text). In the foreground is the test pit from which vertebrate remains were recovered.

transient. These bones suggest the possibility of a breeding population of Cliff Swallows in Barbuda during the late Pleistocene.

The ulna of *Corvus* new sp. from Excavation 2, Two Foot Bay, is the first record of any species of corvid from the Lesser Antilles. The bone is larger than the ulna of the largest living Antillean species, *C. leucognaphalus* of Cuba, North Caicos, Hispaniola, and Puerto Rico, which is known as well from a prehistoric site on St. Croix, Virgin Islands (Wetmore, 1918, 1925, 1937; Olson, 1978). The prehistoric record from St. Croix (also including *C. pumilis*; Wetmore, 1937) is the nearest geographic occurrence for any species of *Corvus*.

The Bahamas Mockingbird (*Mimus gundlachii*) is represented by an ulna and tarsometatarsus from Barbuda I and a femur from Barbuda V. Today this species inhabits semiarid scrub in the Bahamas, cays off northern Cuba, and in southern Jamaica. This relict distribution, which includes late Pleistocene records from Puerto Rico (Olson and Hilgartner,

1982), reflects the fragmentation of arid habitats during the Pleistocene to Holocene transition (Pregill and Olson, 1981). This is the first record of *M. gundlachii* from the Lesser Antilles.

The Brown Trembler (*Cinclocerthia ruficauda*) is represented by four mandibles, a coracoid, ulna, and pedal phalanx from Barbuda I, a coracoid and carpometacarpus from Barbuda V, and two scapulae from Rat Pocket. These specimens, like those from Burma Quarry, Antigua (Steadman et al., 1984a; Pregill et al., 1988), demonstrate that *C. ruficauda*, which is otherwise found throughout the Lesser Antilles, indeed occurred on the Antigua Bank. Furthermore, the Brown Trembler's preference for wet forest may be a post-Pleistocene event that has been exaggerated in recent millennia by habitat modification.

The Forest Thrush (*Cichlerminia lherminieri*) is represented by a tarsometatarsus from Barbuda I and a rostrum from Barbuda V. Like the Brown Trembler, the Forest Thrush prefers humid forest.



Fig. 9.—The Trants archaeological site on Montserrat is an “open” or unsheltered locality situated in a pasture near the island’s east coast.

Today the species is restricted to Montserrat, Guadeloupe, Dominica, and St. Lucia.

The living Puerto Rican Bullfinch (*Loxigilla p. portoricensis*) is confined to Puerto Rico. A large subspecies, *L. p. grandis*, became extinct earlier this century on St. Kitts, the only other island from which the species was ever recorded (Olson, 1984). From Barbuda I we have identified a rostrum and quadrate that represent a form of *Loxigilla* larger than *L. p. portoricensis* and much larger than *L. noctis*, the only species of *Loxigilla* in the Lesser Antilles today. Whereas bones of modern *L. p. grandis* are unavailable, the size of both Barbudan specimens is similar to that of *L. violacea ruficollis* (Greater Antillean Bullfinch) from Jamaica, which, based upon skins, is approximately the size of *L. p. grandis*. The anterior margin of the nares in the rostrum from Barbuda is rounder and forms a more obtuse angle than in *L. noctis*, *L. violacea*, or *L. p. portoricensis*. Otherwise, in such features as curvature of the dorsal

surface and stoutness of the narial bars, the Barbudan specimen is allometrically consistent with an enlarged rostrum and quadrate of *L. p. portoricensis* rather than with a species of *Melanospiza*, *Melopyrrha*, *Tiaris*, or *Loxipasser* (see Steadman, 1982, and Steadman and Morgan, 1986, for intergeneric osteological comparisons). The large races of *L. portoricensis* likely once occurred across the Leeward Lesser Antilles. The survival of one population (on St. Kitts) into this century suggests that much or all of their demise may have occurred during the Holocene rather than the Pleistocene–Holocene transition.

The Grasshopper Sparrow (*Ammodramus saviannarum*) is represented by a complete humerus from Barbuda V. In the West Indies, this small grassland obligate nests very locally on Jamaica, Hispaniola, Puerto Rico, and Vieques, as well as on the marginal islands of Curaçao and Bonaire. It does not occur in the Lesser Antilles today, and its late Pleistocene



Fig. 10.—One of the completed excavation units at the Trants site, Montserrat. Several strata are visible. Numerous faunal remains and cultural artifacts were recovered from this site during research in 1979 and 1990.

presence on Barbuda is another indication of late Pleistocene aridity.

As to mammals, various bats are the only native species that still exist on Barbuda. The large, extinct rice rat (*Megalomys audreyae*) was described by Hopwood (1926) based on a mandible collected around 1900 “among some Pleistocene cave breccia.” No other locality information was provided with the description. Thousands of fossils of rice rats were recovered by the University of Florida researchers and by our team. These specimens are under study by Michael Carlton, U. S. National Museum (USNM).

Finally, bones of 16 species of fish, one testudines, two squamates, three birds, and four mammals were identified from Ceramic Age archaeological sites on Barbuda at Indiantown Trail, Sufferers, and Overview Cave (Fig. 8) (Watters et al., 1984; see Appendix II). These sites produced few examples of the distinctive ceramics characteristic of the initial Saladoid colonization of the Lesser Antilles, which therefore indicates a post-Saladoid occupation start-

ing around the middle of the first millennium A.D. (Watters et al., 1984, 1992).

MONTSERRAT

A small (101 km²) volcanic island (909 m elevation), Montserrat sits atop a single submerged bank midway between Nevis and Guadeloupe, 40 km southwest of Antigua. The island consists of andesitic volcanic rocks which erupted from a succession of centers (Martin-Kaye, 1959; Rea, 1974).

We (GKP, DWS, DRW) visited Montserrat in January 1983, searching unsuccessfully for any feature that might contain noncultural fossil deposits. The only cave discovered was upslope from Broderick's Estate adjacent to the road to Chance Peak, 1 km beyond the estate ruins. None of our test pits yielded bone. Apparently the sediments, and probably the cave itself, are of modern origin, being an expansion of the ghaat at the mouth of the cave that resulted from erosion when the surrounding hillsides were cleared for agriculture and pasture.

Montserrat has, however, yielded vertebrate fau-



Fig. 11.—Basse Terre, Guadeloupe, is a steep volcanic island in the middle of the Lesser Antillean inner arc. The view in this photo is from Mourne à Louis looking east toward the limestone half of Guadeloupe, Grande Terre.

nas from archaeological sites at Trants (Fig. 9, 10) and Radio Antilles that correspond with the early Ceramic Age Saladoid migration to the Lesser Antilles 2,500 years ago (Watters, 1980; Steadman et al., 1984b; Petersen and Watters, 1991). In addition to at least 12 species of fish, these sites yielded marine turtles (*Cheloniidae* sp.), *Iguana* sp., nine birds (none extirpated), and six or seven mammals that included an uncertain variety of undescribed rice rats (*Oryzomyini* spp.). There are additional specimens of undescribed rice rats from Montserrat in the USNM mammal collections (USNM 240852, received March 1924 from Seymour Wylde Howes). The preservation of these specimens would suggest a cultural context, most likely the Trants site where Howes was the estate manager.

GUADELOUPE

Guadeloupe, the largest island in the Lesser Antilles, lies 60 km south of Montserrat. The eastern half, Grande Terre (567 km²) is a limestone cap with significantly greater paleontological potential than the volcanic western half, Basse Terre (945 km²),

which is steep, dominated by peaks to 1,350 m, and shrouded in most of Guadeloupe's wet forest (Fig. 11).

The only reference to fossil vertebrates from Guadeloupe is that of midden material from the coastal, prehistoric Ceramic Age site at Morel à Moule (Fig. 12) that was excavated by Edgar Clerc (1968; see also Barbotin, 1970). The bones consisted of iguana, undetermined birds, small mammals including *Oryzomys* (given as *Oryzomis mégalomis* [sic]), and agouti. Wing et al. (1968) mentioned this undescribed rice rat in their study of vertebrate remains from the Mill Reef archaeological site on Antigua.

One of us (GKP) conducted a field reconnaissance of Guadeloupe from 9–19 March 1984 to look for noncultural fossil sites. On Basse Terre, GKP investigated a few small caves at Trou Caverne, a boulder-strewn hillside north of Pointe Noir, and a series of shallow overhangs along the roadside between Basse Terre and Vieux Fort. None of these localities is important paleontologically. Along the northeast coast of Grande Terre between Pointe de la Grande Vigie and Moule are numerous sea caves,



Fig. 12.—There are numerous coastal archaeological sites in the Lesser Antilles, such as Morel à Moule, Grande Terre, Guadeloupe. Natural processes like coastal erosion have imperiled this and similarly situated localities.

overhangs, and cliffs. Only the few small caves at Anse Maurice contained any dry sediment. One of these yielded surface bones of *Rattus* (a European introduction), but nothing else.

Two noncultural sites on Grande Terre (Fig. 13) yielded some fossil material of interest, although other prospective localities remain, especially in the hilly region of Les Grand Fonds. One of these two sites is a shallow pocket (ca. 0.3 m²) located against the back of a narrow cliff overhang, about 0.5 km south (inland) from Pointe du Capucin at the northernmost extent of Grande Terre. The cliff defines the south wall of a narrowing gorge with dense second growth forest (Fig. 14).

The second site is a small cave located on the south coast of Grande Terre, in the brush-covered hillside approximately 200 m inland from the sea cliffs. It is 3.9 km west of St. Francois, and 0.6 km east of Pointe du Vent. The low, narrow opening must be entered on hands and knees, but gives way immediately to a steep descent over loose rock and rubble, and then opens into a chamber less than 2 m high. The floor is damp and rocky and measures approximately 5 × 7 m. Daylight penetrates into

the chamber through a small opening in the ceiling below the northeast wall. About 3 m east of the entrance is a small deposit of dark brown, relatively dry sediment that extends to a depth of approximately 25 cm.

Bones of two frogs, four lizards, and a snake were recovered from the Pointe du Capucine locality and at Pointe du Vent. Numerous bones of bats also were present in the Pointe du Vent fauna, but these have not been studied. Both of these deposits most likely date to the Historic Age, although neither contained human artifacts. The shallow accumulation of sediment at Pointe du Capucine contained bones of *Rattus* throughout. Bones of *Rattus* sp. and another post-European species, *Bufo marinus*, were present at the Pointe du Vent site, but they were mostly confined to the upper half of the test pit. The reptile and amphibian bones are described below.

Anura

Bufo marinus

Pointe du Vent.—3 vertebrae, 1 humerus. MNI = 1.

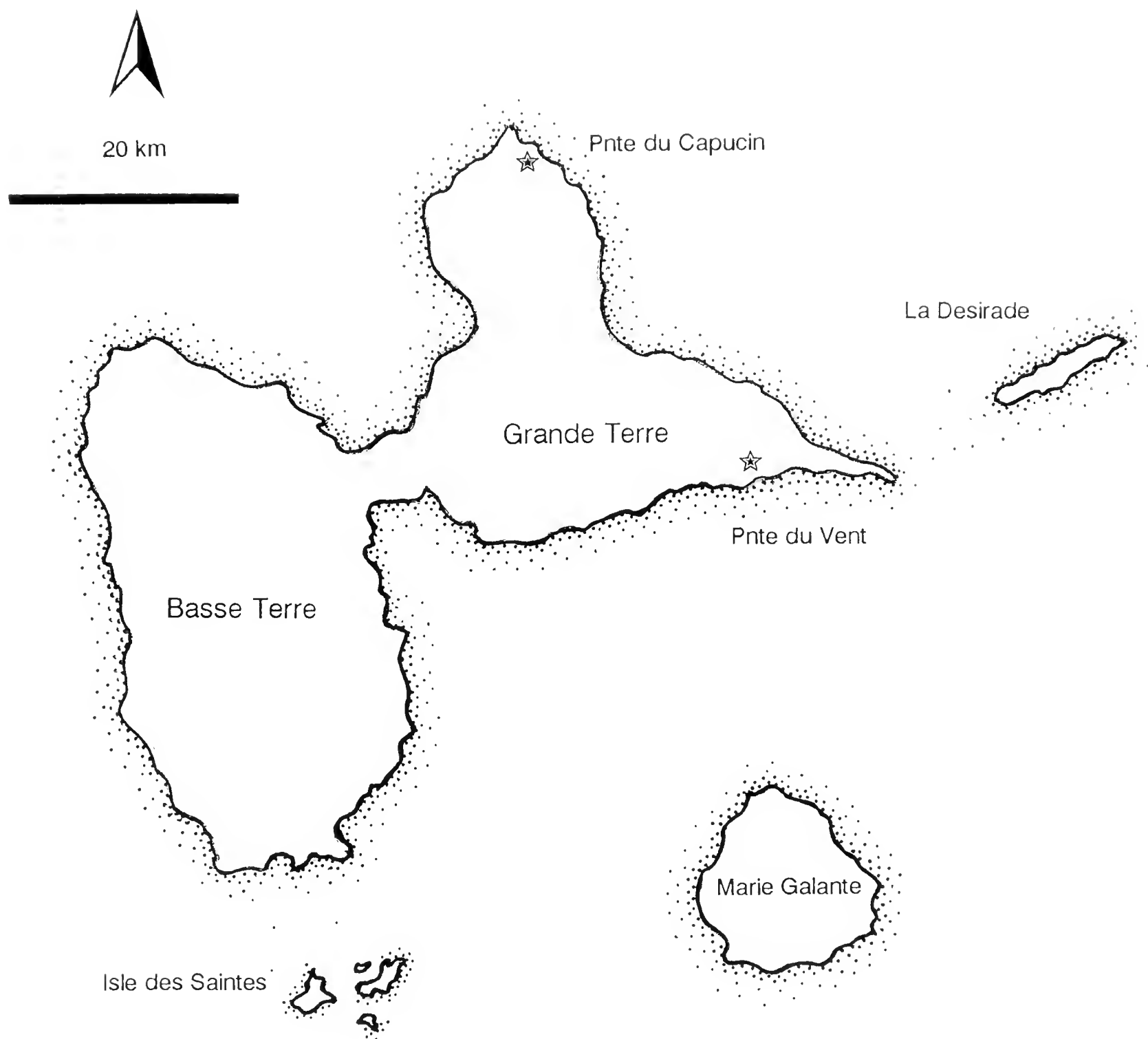


Fig. 13.—The twin island of Guadeloupe showing the location of the two noncultural vertebrate localities at Pointe du Capucine and Pointe du Vent. The fossils of amphibians and reptiles from these sites are described in the text.

The Cane Toad was introduced into Martinique and Barbados prior to 1850. It has become established on most of the larger islands in the Lesser Antilles, including Guadeloupe (Easteal, 1981). The circumstances surrounding its dispersion throughout the Windward and Leeward Islands is unclear, although the majority of introductions were purposeful and probably occurred before 1900. Populations on several islands may be the result of more than one introduction. *Bufo marinus* was present early this century on Grenada, Barbados, St. Lucia, St. Kitts, Martinique, Nevis, and Montserrat (Bar-

bour, 1914). It may not have become established on Guadeloupe and Dominica until later.

Eleutherodactylus cf. *E. martinicensis*

Pointe du Capucine.—27 ilia. MNI = 18.

Pointe du Vent.—2 quadratojugals, 9 mandibles, 2 scapulae, 24 vertebrae, 33 ilia. MNI = 16.

These remains of an eleutherodactyline frog(s) came from individuals with a range of 28–35 mm svl. Undiagnosed to species level, the bones are referred to *E. martinicensis* because it is the only native species of *Eleutherodactylus* found on Grand



Fig. 14.—The vertebrate fossil locality at Pointe du Capucine, Guadeloupe, is a mere cliff overhang on the south wall of a narrowing gorge choked with second growth forest.

Terre; *E. johnstonei* is a recent introduction. On Basse Terre *E. barlagnei* (Lynch, 1965, svl ca. 32 mm) is limited to bouldered streams in the upland forest, and the smaller (svl ca. 20 mm) *E. panchoni* occurs in mesic forest at elevations between 200–700 m (Schwartz, 1967).

Squamata

Hemidactylus mabouia

Pointe du Vent.—7 dentaries, 4 maxillae, 3 frontals, 1 parietal, 12 vertebrae. MNI = 4.

The bones are indistinguishable from those of comparative skeletons of *H. mabouia* that GKP collected from Guadeloupe. The largest fossil dentary has a tooth row that measures 7.8 mm and came from an individual with svl of about 60 mm, which is comparable to modern adults of this species.

Hemidactylus mabouia is widely distributed in the neotropics, in large measure because of its edificarian tendencies and easy transport by humans.

It ranges along the eastern coast of South America, from Uruguay north into Tobago and Trinidad, throughout the Lesser Antilles, the Puerto Rican bank, Haiti (Port-au-Prince), and Cuba (Guantánamo). It has not been reported previously in a fossil context. Kluge (1969) argued that *H. mabouia* was present in the West Indies prior to the days of slave trading, and is probably indigenous. Although the deposits from Pointe du Vent lack a chronology, they do provide some verification of a historical presence of *H. mabouia* in the Lesser Antilles.

Thecadactylus rapicauda

Pointe du Capucine.—5 dentaries, 6 maxillae, 3 premaxille, 4 quadrates, 2 prefrontals, 1 pterygoid, 15 thoracic vertebrae. MNI = 3.

Bones of this large gecko are identified by their greater size and peculiarities of dentition (see account of this species in the Anguilla section). The largest dentary has a tooth row length of 14.7 mm

and came from an individual estimated at 95 mm svl. Other fossil occurrences of *Thecadactylus rapicauda* are Anguilla (above) and the Antigua Bank (Etheridge, 1964; Pregill et al., 1988).

Anolis marmoratus

Pointe du Vent.—29 dentaries, 7 articular + surangular, 10 maxillae, 1 quadrate, 6 frontals, 3 basalia, 2 pterygoids, 3 postorbitals, 6 pelves. MNI = 16.

Pointe du Capucine.—42 dentaries, 19 maxillae, 1 premaxilla. MNI = 25.

None of these fossils differs from comparable skeletal elements of living *Anolis marmoratus*, the only species of anole on Guadeloupe. The largest individual from both fossil sites has an estimated svl of 60 mm. Lazell (1972) recognized two subspecies on Grande Terre: *A. m. speciosus* occupying the southwestern portion of the island and the isthmus (males to 73 mm svl), and *A. m. inornatus* in the northern half (males to 65 mm svl).

Iguana sp.

Pointe du Vent.—1 dentary fragment, 1 articular, 1 partial pterygoid, 7 vertebrae, MNI = 1.

These elements are easily referred to a species of *Iguana* by their size and morphology. While osteological details of the articulated skull distinguish *Iguana iguana* from *I. delicatissima*, none of the fossils is sufficiently complete for species-level identification. Both species occur erratically throughout the Lesser Antilles, and are sympatric only on Les Îles des Saintes off the southern coast of Basse Terre. *Iguana delicatissima* is found from Anguilla south to Martinique, whereas *I. iguana* ranges from the Virgin Islands south to the Venezuelan coast, and on the mainland from Mexico to southern Brazil and Paraguay. Both species may well have been on Guadeloupe, although only *I. iguana* is found there now. Iguanas have become restricted in most areas of the Lesser Antilles because of habitat destruction and predation. The present distribution of either species probably does not reflect its prehistoric range (Steadman et al., 1984b).

Leiocephalus cf. *L. cuneus*

Pointe du Capucine.—1 dentary, 1 maxilla, 1 sacral vertebra. MNI = 1.

These bones of *Leiocephalus* are described in detail elsewhere (Pregill, 1992). As with the Anguilla specimens of this lizard (above), they can be referred

only tentatively to the extinct *L. cuneus*. The dentary from Pointe du Capucine has a tooth row measuring 12.4 mm and came from an individual with an estimated svl of 110 mm. The fossils mark the southernmost occurrence of *Leiocephalus* in the Lesser Antilles, other than the now extinct *L. herminieri* presumed to have come from Martinique (Pregill, 1992). It is interesting that the bones were found among those of *Rattus* in no more than a few centimeters of dusty sediment, suggesting that *Leiocephalus* persisted on Guadeloupe into historical times, but became extinct before collectors could secure any specimens.

Ameiva cf. *A. cineracea*

Pointe du Vent.—2 maxillae (1 large, 1 small), 7 thoracic vertebrae. MNI = 2.

Pointe du Capucine.—1 maxillary fragment, 1 caudal vertebra. MNI = 1.

Two adults and a juvenile are represented by this material, referred to *Ameiva* based on numerous details of the jaws and dentition (see Pregill et al., 1988). The adults were at least 150 mm svl. The fossils are too fragmentary for specific identification, and are provisionally referred to *A. cineracea* Barbour and Noble (1915) because it is the only species of *Ameiva* known from Guadeloupe. The type series and only known specimens of this lizard consist of a male and two females collected from Grand Isle, a small spit of land located a few hundred meters off Petit Bourg, Basse Terre. The species is now extinct, and probably was declining when initially discovered. Barbour and Noble (1915:455) commented that on this tiny islet "only 50 yards in extent . . . there certainly cannot be more than a dozen or two of these *Ameiva*." The most recent taxonomic treatment of *A. cineracea* is that of Baskin and Williams (1966), who considered the species distinct from other Lesser Antillean ameivas, but noted consistent similarities with the now extinct *A. major* Dumeril and Bibron from Martinique. Although *A. cineracea* has never been recorded from either Basse Terre or Grande Terre, the fossils demonstrate that *Ameiva*, regardless of species, was widely distributed at least on Grande Terre until quite recently.

Typhlops cf. *T. dominicana guadeloupensis*

Pointe de Capucine.—23 vertebrae. MNI = indeterminate.

These small vertebrae with flat, low profiles and

lacking neural spines are easily referable to a species of *Typhlops*. The largest vertebrae measure 4.0 mm across the prezygapophyses, have a centrum length of 2.5–3.0 mm, and came from an individual(s) of about 300 mm svl. These bones are referred to *T. dominicana guadeloupensis* because it is the only species of blind snake known from Guadeloupe. It is poorly represented in collections. The holotype (CM 41216) was taken 2 km southwest of Port-Blanc, Grande Terre (Richmond, 1966). Thomas (1976) secured additional specimens from several localities on both Grande Terre and Basse Terre.

cf. *Alsophis antillensis*

Pointe du Vent.—14 vertebrae. MNI = indeterminate.

Pointe du Capucine.—23 vertebrae. MNI = indeterminate.

These vertebrae are from very small juveniles to large adults. They conform in most respects to vertebrae of *Alsophis antillensis*, but differences in vertebral structure are subtle between that species and the only other colubrid from Guadeloupe, *Liophis juliae*. The neural processes of *A. antillensis* are thinner and not as tall. The largest fossil (Pointe du Vent) has a centrum length of 5.0 mm and measures 9.4 mm across the tips of the accessory processes. The bone came from a snake with an estimated svl of 850–950 mm.

There is no recent information on the population status of *A. antillensis* on Guadeloupe. On mongoose-infested islands like this one it is not commonly encountered, and supposedly none had been collected in many years. GKP obtained a juvenile specimen (SDSNH 64422) in the vicinity of Grands-Fonds, Grande Terre, in March 1984. Fossils referred to this species are known from Barbuda (above), and from Antigua (Pregill et al., 1988) where it has become extinct except on tiny Great Bird Island (Lazell, 1967; Henderson, 1989). *Liophis juliae* is also rare on Guadeloupe and was believed to be extinct at one time. However, specimens were collected by Albert Schwartz a few years prior to Dixon's (1981) taxonomic treatment of the insular species of *Liophis*. Still, the total number in collections is probably no more than ten. *Liophis juliae* also occurs on Marie Galante and Dominica.

MARIE GALANTE

Neither of the two small archaeological faunas known from this island (150 km²) adjacent to Gua-

deloupe has been described in detail. The fauna from the Folle Anse site was mentioned by Barbotin (1970, 1976) and tabulated by Wing (1973), who compared it in relative abundance and diversity to archaeological faunas from the Sugar Factory site on St. Kitts (Hoffman, 1973; Wing, 1973) and the Mill Reef site on Antigua (Hoffman, 1973). Compared to Mill Reef, both the Sugar Factory site and the Folle Anse site contain a higher percentage of fish such as grouper and tuna, presumably indicating deeper near-shore water. The terrestrial fauna from Folle Anse included agouti, an unidentified extinct rice rat (*Oryzomyini* sp.), the historically introduced pig (*Sus scrofa*), and several indigenous birds and reptiles of little biogeographic importance.

A second vertebrate assemblage from Marie Galante was excavated at the Talisronde site (Barbotin, 1970), and mentioned in Wing and Scudder's (1980) report on the bones from the Sugar Factory Pier and Cayon sites on St. Kitts. Wing and Scudder (1980) did not provide a list of species from Talisronde, only noting that approximately 24% of the vertebrae are terrestrial (including beach habitat) species. They regard the Talisronde site as contemporaneous with the early occupation of the two St. Kitts localities, and with the Mill Reef site on Antigua.

No noncultural vertebrate fossils are known from Marie Galante, but as it is a limestone island much like the Grande Terre half of Guadeloupe, deposits could be expected.

DOMINICA

No fossil vertebrates have been reported from this island.

MARTINIQUE

Two early, and one more recent, collections of vertebrate fossils are known from this volcanic island, the second largest in the Lesser Antilles (1,101 km²). The first of these faunas includes fish, reptiles, birds, and mammals found beneath a lava flow at Anse-Belleville that were announced in a preliminary report by Friant et al. (1940). The material undoubtedly represents the remnants of an Amerindian midden although the age was never determined. The two reptiles—Hawksbill (*Eretmochelys imbricata*) and large iguana (cf. *Iguana*)—were described in more detail by Hoffstetter (1946); the agouti (*Dasyprocta* sp.) and the extinct, large rice rat

(*Megalomys desmarestii*) were described by Friant (1941). The fish were treated by Chabanaud (*in* Friant et al., 1940). According to a footnote in Hoffstetter (1946), Chabanaud was also studying the bird bones, but that account was not published.

The other early collection of vertebrate fossils is from the Paquemer archaeological site at the south-eastern end of the island, excavated during 1947–1951 by Père R. Pinchon (Wetmore, 1952). The Black-capped Petrel (*Pterodroma hasitata*) and four other species of birds (*Buteo platypterus*, *Porphyryula martinica*, *Zenaida aurita*, and *Columba squamosa*) were reported, along with associated bones of “turtle, iguana, and extinct mammals” (Wetmore, 1952: 460).

The more recent fauna is from the Macabou archaeological site—a Ceramic Age site containing Suazoid series ceramics—on the southeast coast of Martinique near the town of Vauchin (Allaire, 1977: appendix I; Fraser, 1981). Vertebrates were excavated from a small shell midden (called “Area F”) and tabulated by Fraser (1981). Besides the 13 species of fish, there were bones of the extinct rice rat (*Megalomys desmarestii*), agouti (identified as *Dasyprocta* cf. *D. cristatus*), and manatee (*Trichechus* sp.). In her table Fraser (1981:56) also listed “large mammal,” “medium-large mammal,” “small-medium mammal,” and “small rodentia.” No further identification of these mammals was provided, nor any indication of whether they represent distinct taxa. Likewise, tabulated without comment or diagnosis are: Cheloniidae, small Cheloniidae, Cheloniidae sp., *Lepidochelys*, Iguanidae, and a single bird bone as “medium aves.” Fraser’s (1981) report included a tabulation of vertebrates from “Area B” of the Macabou site that was based on an unpublished account by Elizabeth Wing in 1974. In addition to those taxa from “Area F,” the remains consisted of *Caretta caretta* and two birds, one of which was identified as *Limnodromus griseus*. In addition, Allaire (1977) lists the post-European *Bos taurus* from Macabou I.

ST. LUCIA

The only published account of vertebrate remains from this lush volcanic island (603 km², elevation 953 m) south of Martinique is a comparative study of aboriginal fishing practices (Wing, 1968). The Grand Anse site on St. Lucia was excavated by William G. Hagg and Ripley Bullen. Bones of 201 individual vertebrates were reported, and approximately half of these were fish. Marine turtles were

tabulated only as Cheloniidae, although *Chelonia mydas*, *Eretmochelys imbricata*, and *Caretta caretta* were listed in a footnote (Wing, 1968:105). The only other reptile was *Iguana* sp. (*I. iguana* occurs on St. Lucia today). The fauna also included bones of an unidentified bird(s?), and the following mammals: *Didelphis marsupialis*, *Dasyprocta* sp., the extinct large rice rat *Megalomys luciae* (= *Oryzomys luciae* Major, 1901), and dog. McKusick’s (1960) study of St. Lucia’s prehistoric site contains no information on vertebrates.

ST. VINCENT

In the company of Ronald I. Crombie and Thomas Parsons, GKP searched this volcanic island (214 km², 1,290 m elevation) for two weeks in August 1989, hoping to locate fossil-bearing sediment. There are a few caves that are well-known locally because of their petroglyphs. The largest cave, which is actually an overhang approximately 6 m high, 10 m long and 4 m deep, is situated in an expansive volcanic cliff that encloses the south side of Buccament Valley, St. Patrick Parish. The soil is deep but very organic. Two test pits of 1 m depth yielded only a few surface scraps of domestic animals such as goats and cats. No other cave sediment was found on St. Vincent.

Vertebrate remains are not mentioned from 11 prehistoric sites on St. Vincent reported by Bullen and Bullen (1972). More recent work at one site, Buccament Rockshelter, included fine-mesh screening of samples from the Bullens’ south profile as well as from deeper levels previously unexcavated (Hackenberger, 1991). The recovered material consisted of “. . . one very small bone fragment and two small fish vertebra” (Hackenberger, 1991:89). Bullen and Bullen (1972:30) noted “. . . some fragments of turtle bones” from the Mayreau Island Beach site in the Grenadines between St. Vincent and Grenada.

BARBADOS

Barbados (430 km², 370 m elevation) is unusual in the southern Lesser Antilles in that its composition is entirely nonvolcanic. Approximately 75% of the area consists of successions of concentric coral reef terraces uplifted during the Pleistocene (Bender et al., 1973; Matthews, 1973; Bard et al., 1990; Guilderson et al., 1993). With further study, the relative youth of Barbados could provide a valuable chronological reference point from which to evaluate the dispersal, colonizing ability, and *in situ*

evolution of various terrestrial taxa (e.g., Peck, 1981).

Little vertebrate paleontology has been done on Barbados despite its potential. No field investigations have been conducted there in the past 25 years, and the only noncultural vertebrate fossil site known is at Spring Bay, St. Philip Parish. Swinton (1937) reported remains of *Iguana iguana* and a small oryzomyine rodent that had been collected by C. T. Trechmann from cavities at the base of coralline limestone cliffs below the Ragged Point Lighthouse. Neither iguanas nor rice rats are known historically from Barbados (Ray, 1964a; Marsh, 1985). In 1963 the area was investigated by Clayton Ray whose field party collected more bones from fissures in the same limestone formation. The majority of the bones represent terrestrial species of probable late Pleistocene or Holocene age. The marine vertebrates represented (shark teeth, teleost fish, and a cetacean periotic) are believed to have been redeposited from Miocene marine sediments (Ray, 1964a).

Ray (1964a) also listed a tortoise, cf. *Geochelone* (extinct); the lizard *Anolis roquet* (= *A. extremus*); the snake *Leimadophis* (= *Liophis*) *perfuscus*; a dozen bird bones described in the same journal by Brodkorb (1964); and two mammals, a porpoise (Delphinidae) and cricetid rodent (*Oryzomys* new sp.). Of the six species of birds, only two still occur on Barbados: *Puffinus lherminieri* and *Dendrocygna autumnalis*. Other bird bones represented two supposedly extinct species: a sheldgoose *Neochen* "*barbadiana*" (see account of Barbuda above), and the coot *Fulica podagrica* (which may not be distinct from living species [Olson, 1974, 1977]). Finally, there were bones of the West Indian Whistling Duck (*Dendrocygna arborea*), which had not been recorded from Barbados, and Red-tailed Hawk (*Buteo jamaicensis*), an extirpated species known on Barbados from historical records.

There are also remains of vertebrates from four cultural sites on Barbados that were inhabited by Suazoid occupants of the island (Wing, 1991). The majority of the bones were recovered at Heywoods, followed by sites at Hillcrest, Silver Sands, and Chancery Lane. A pooled tabulation of these four sites listed the reptiles *Chelonia mydas*, additional unidentified sea turtles, and an unidentified colubrid snake (suggested to be the resident species *Dromicus* [= *Liophis*] *perfuscus*). The bird bones were identified as *Aythya collaris*, *Dendrocygna* sp., Columbidae sp., *Gallus gallus* (a post-European introduction), *Porphyryula martinica*, and *Mimus* sp. Other

than rice rats, the remains of mammals comprised nonnative species (pig, sheep, dog).

GRENADA

Grenada (214 km², 889 m elevation) abounds in archaeological sites, which thus far have been its only source of late Quaternary vertebrate remains. Bullen's (1964) archaeological summary of Grenada listed 14 sites, of which the most important are Savanne Suazey, Pearls, Calivigny Island, and Westerhall Point. The terrestrial vertebrates recovered were identified as *Iguana* sp., *Chelonia mydas*, *Didelphis marsupialis*, *Dasyprocta* sp., *Canis familiaris*, and *Homo sapiens*.

Recent excavations at Pearls (Cody, 1991) have recovered more bones, about 10% of which are mammals (Lippold, 1991). These include a large and small species of rice rat that are believed to correspond in size to *Oryzomyini* sp. A and sp. B from Montserrat (Steadman et al., 1984b), the agouti, opossum, and dog (Lippold, 1991). Other recent material from Pearls includes three species of birds *Puffinus lherminieri*, *Pelecanus occidentalis*, and *Pandion haliaetus*, and the armadillo *Dasyurus novemcinctus* (Fandrich, 1990).

Since it is volcanic and mountainous, Grenada has few dry caves or shelters suitable for preserving bone in owl pellets. Some limestone occurs at the north end of the island at Mt. Rodney and Mt. Alexander, although solution features were not evident here during a reconnaissance by GKP in July 1990. Caves or cave-like features were found in only three places on Grenada. One is an unnamed, almost vertical shaft located near the center of the Grand Etang Forest Reserve. It appears to have formed from a collapsed lava tube, but since it is in the wet, upland forest (ca. 730 m elevation) it is far too damp for dry sediment to have accumulated.

Elsewhere there is a series of shallow caves formed in the cliff overhangs near Little Bacolet Point, St. David Parish. Little Bacolet Point is one of numerous headlands jutting from the south coast of Grenada. The road heading seaward (south) to the end of the point parallels a wooded stream on the east and a high, broken escarpment on the west. The escarpment rises to about 50 m above the road, and is set back from the road approximately 75 m across a hill covered in dense scrub. The escarpment and cliffs extend for about 0.5 km north-south. The base of the cliff is eroded into shallow (<50 cm) recesses

packed with dry, powdery sediment. No bone was found in the several test pits that were screened.

The only significant cave GKP encountered on Grenada is located 0.4 km inland from the south side of Black Bay, St. John Parish, along a forest margin adjacent to a large pasture. The entrance, partially blocked by rubble, is approximately 2 m high and 4 m wide. The cave itself is a tunnel of these same dimensions that extends horizontally for about 25 m before terminating abruptly. Here, a shaft of dull light is cast through a shallow opening in the ceiling, partially illuminating the numerous bats that roost in the back half of the cave. Supposedly the cave walls and ceiling were quarried during the French occupation of the island in order to provide storage and standing room (Thomas J.

Banks, personal communication). In any case, while the cave would have been a suitable roost for barn owls, no evidence of current use by owls was detected.

The floor is dry and composed of moderately organic volcanic dust and abundant gravel to a depth of 5–20 cm. The deepest sediments are near the entrance. The few isolated bones of lizards from the top of this layer represent species still living in or near the cave (*Thecadactylus rapicauda* and *Anolis aeneus*). Out of five test pits, only one could be excavated into strata below the surface layer before encountering bed rock, about 1 m deep. Most of the deeper sediment was composed of partially indurated gravel-size volcanics. No bones were found.

DISCUSSION

Although vertebrates are briefly noted in some of the older archaeological reports on the Lesser Antilles (e.g., Branch, 1907; Josselin de Jong, 1947), only in the past 25 years have archaeologists used screening techniques with regularity to sample faunal remains. The thorough analysis of these faunas by zooarchaeologists is equally recent (Watters, 1989). Compared with the Greater Antilles, there are far fewer paleontological sites in the Lesser Antilles, but an abundance of archaeological sites. Of the 48 vertebrate localities reviewed, 33 (69%) are Amerindian middens found in prehistoric archaeological sites (Table 1). Paleontological specimens, however, were being deposited before, and continued to be deposited during and after human colonization of the Lesser Antilles. The primary paleontological sources are unindurated and occasionally indurated sediments in caves, sinkholes, and fissures, in which bone concentrations derive mainly from owl pellets. The owls included both living and extinct species of *Tyto* (barn owls), and *Athene cunicularia* (Burrowing Owl), which consumes prey species of a smaller size on average. Natural traps also account in part for some of the fossil deposition, especially for large-bodied species.

Bone in archaeological contexts results from human activity. In the Lesser Antilles human occupation has persisted for at least four millennia. The first 3,500 years is represented by the prehistoric (pre-Columbian) period, when the inhabitants were Archaic Age and Ceramic Age Amerindians. Non-

Amerindian inhabitants (Europeans and Africans) have been in the Lesser Antilles for about the past 500 years, the post-Columbian period.

The scarcity of vertebrate data from the oldest (ca. 2000–500 B.C.) of the prehistoric sites (Archaic Age) in the Lesser Antilles means that the first 1,500 years of contact between humans and indigenous vertebrates remain, for the most part, unknown. An exception is part of the vertebrate assemblage from Burma Quarry, Antigua, which has excellent stratigraphic and chronological control (Steadman et al., 1984a; Pregill et al., 1988). The lower vertical unit at Burma Quarry, with a wood charcoal ^{14}C date of $4,300 \pm 150$ yrs B.P., may correspond chronologically with the earliest settlement of the island by Archaic Age peoples. We summarize the distribution of extinct versus living vertebrates at Burma Quarry in Table 2. Each of the ten extinct species recovered from chronostratigraphically secure units occurred in the lower vertical unit. In spite of a larger sample of identified bones, only five of these species were recorded from the east and west horizontal units, which are about 500–1,000 years younger than the lower vertical unit. The only other Archaic Age sites with data on vertebrates, albeit limited, are Hichmans' Shell Heap and Nisbetts on Nevis.

The other archaeological vertebrate faunas discussed in this paper are restricted almost exclusively to Amerindian occupation during the Ceramic Age, ca. 500 B.C. (= 2,500 years B.P.) to A.D. 1500. The better-represented faunas include early Ceramic Age

(i.e., Saladoid) sites such as Trants on Montserrat and Sugar Factory Pier on St. Kitts, as well as later sites like Heywoods on Barbados. Most of the early and late Ceramic Age faunas are from open sites that were once villages; Golden Rock, St. Eustatius, and Trants on Montserrat (Fig. 9, 10) are good examples of open sites. Only a few faunas are from closed sites (caves and rockshelters) such as Fountain Cavern, Anguilla, and Overview Cave, Barbuda (Fig. 8).

Vertebrate faunas have not been reported from archaeological sites dating to the third chronological period, the Historic Age beginning at about A.D. 1500. In the Lesser Antilles, excavation of historical sites is a recent endeavor that has not yet provided information on vertebrates. Such data would help to document the vertebrate fauna at the time of European colonization and the subsequent introduction of alien species. Animals such as goats, pigs, rats, and chickens occasionally appear in faunal lists of prehistoric sites (e.g., Overview Cave, Barbuda), but they are always from the uppermost, disturbed levels in which prehistoric and historic materials are mixed. Introduced species, particularly *Rattus*, also are found in contexts where evidence of human involvement is absent, for instance at Pointe du Vent and Pointe du Capucine, Guadeloupe.

The vertebrates that occur only or primarily in cultural contexts attest to their use as food by Amerindians. Sea turtles (Cheloniidae) and domesticated mammals such as the agouti (*Dasyprocta* sp.) are frequent examples. Moreover, the agouti, and probably iguanas, were transported between islands by humans to ensure their availability for future consumption. By contrast, nearly all occurrences of bats, lizards other than iguanas, hummingbirds, and passerines occur in noncultural deposits. The extinct rice rats (*Oryzomyini* sp.) are amply represented in cultural and noncultural contexts with nearly equal frequency; these medium- to large-sized rodents were savory prey for owls and humans alike. There are also similar instances of various columbids (pigeons and doves) and Audubon's Shearwater occurring regularly in both cultural and noncultural deposits.

Human-engendered extinction or extirpation characterizes the Lesser Antillean vertebrate fauna, as is the case for other islands around the world. Archaeological and paleontological studies in Polynesia (e.g., Pregill and Dye, 1989; Steadman, 1989; Kirch et al., 1992) demonstrate that human colonization of previously uninhabited islands can lead to rapid extirpation of birds and large-bodied liz-

ards. For the Lesser Antilles, the distinction is that impact by initial Amerindian colonization on the indigenous vertebrates remains largely unknown because there are so few faunal studies for the first 1,500-year span of the Archaic Age (2000–500 B.C.). It is equally difficult to estimate which and how many species persisted into the Historic Age on a given island. For instance, only two of the 15 extinct or extirpated species of reptiles with a fossil record (Table 6) are known historically by specimens from their respective island. Six others are extant elsewhere and seven are known only by fossils. Considering the vertebrate fossil record as a whole, 79 indigenous species or populations (exclusive of fish) have become extinct on islands from which fossil specimens of them are known. Thirty-one are known only by fossils, whereas the other 48 are either extant elsewhere but without a historic record from that island (39), or are known historically from that island (9). As with squamates, some of the 39 species of birds and mammals that lack historic records may have persisted into post-Columbian times only to vanish before collectors became aware of them. Numerous species of Lesser Antillean squamates are known only from the holotype or type locality, have been rare since they were discovered and described, and still others like *Ameiva major* and *Leiocephalus herminieri* have become extinct in the past two centuries, as has the large native frog *Leptodactylus fallax* (Schwartz and Thomas, 1975; Schwartz and Henderson, 1988). *Leptodactylus fallax* is known historically by specimens from St. Kitts, Montserrat, Guadeloupe, Dominica, and St. Lucia (Heyer, 1979); today it is extant only on Dominica and Montserrat.

There are additional species of vertebrates, although lacking a fossil record, that have become extinct historically and are known only from one or a few specimens. Examples are the rodent *Oryzomys victus* (St. Vincent) and the lizards *Leiocephalus herminieri* and *Ameiva major*, both presumably from Martinique. Most, and perhaps all, populations of oryzomine rodents in the Lesser Antilles disappeared some time after colonization by humans and/or *Rattus*. On the other hand, species of *Ameiva* and populations of the snake *Alsophis antillensis* in the Lesser Antilles have both survived and vanished inconsistently.

The extinction of some species that are known only by fossils, and lacking unequivocal evidence associating them with humans, may be related to changes in climate, vegetation, land area/sea level,

or other nonanthropogenic events associated with the glacial-interglacial transition about 12,000 years ago. Sea-surface temperatures 19,000 years ago, as determined from oxygen isotope studies of corals from Barbados, were 5°C cooler than present (Guilderson et al., 1993). About 4°C of this change occurred from only 13,700–12,000 years ago. The presumed late Pleistocene sites on Barbuda have yielded at least four species of birds that are strong indicators of semiarid scrub, savannas, grasslands, or some mix of these nonforested habitats (see detailed discussion based mainly on Puerto Rican and Bahamian faunas in Pregill and Olson, 1981). These four species, all of which are otherwise known only from the Greater Antilles, are *Burhinus* cf. *B. bistrictus*, *Athene cunicularia*, *Mimus gundlachii*, and *Ammodramus savannarum*. Assuming that these semiarid habitats graded into dry forest on parts of the island, then a mosaic of dry forest, scrub, and grassland on late Pleistocene Barbuda could have sustained the entire assemblage of 29 species of birds listed in Table 4. Nearly half (14) of these species no longer occur on the island. Understanding the chronology of extinctions on Barbuda will depend upon ¹⁴C dating of many fossil sites.

Other species whose extinction is problematic include one, and possibly two, species of tortoise from Sombrero and Barbados; the large iguanid from Barbuda that probably represents an extinct species of *Cyclura*; a boid snake (cf. *Boidae*) from Antigua; a parakeet (*Aratinga* new sp.), barn owl (*Tyto* sp.), and raven (*Corvus* new sp.) from Barbuda; a sheld goose (*Neochen* cf. *N. jubata*) from Barbuda and Barbados; a taxonomically dubious coot (*Fulica podagrica*) from Barbados; and the giant rodent *Amblyrhiza* from Anguilla and St. Martin. MacPhee et al. (1990) believed that *Amblyrhiza inundata* may have become extinct well before human contact because no fossils of this rodent are known from cultural deposits. Also, the fossil-associated calcite from an *Amblyrhiza* locality on Anguilla was dated (uranium series) at slightly over 100,000 years B.P. We add, however, that a rodent as immense as *Amblyrhiza* would be unlikely to survive very long after human arrival. Until there is a more nearly complete faunal record from the first few centuries of human presence on Anguilla and St. Martin, the cause of the extinction of *Amblyrhiza*, as well as these other taxa, will remain conjectural.

There are also a few instances of extinction that are less easily attributable directly to human activity, despite the association of fossils in a cultural

Table 6.—*Extinct and extirpated amphibians and reptiles of the Lesser Antilles. Taxa indicated by an asterisk have no fossil record and have become extinct historically.*

| | Extinct on island, historic record | Extinct on island, no historic record | Extinct, known only by fossils |
|--|---|--|--------------------------------------|
| <i>Leptodactylus fallax</i> (St. Kitts, Guadeloupe, St. Lucia) | x | | |
| <i>Geochelone sombreroensis</i> (Sombrero) | | | x |
| <i>Geochelone</i> sp. (Barbados) | | | x |
| <i>Anolis bimaculatus</i> giant morph ¹ (Antigua, Barbuda) | | | x |
| <i>Anolis watsi</i> (Anguilla) | x | | |
| cf. <i>Cyclura</i> sp. (Barbuda) | | | x |
| <i>Iguana delicatissima</i> (St. Kitts) | | x | |
| <i>Iguana iguana</i> (Barbados) | | x | |
| <i>Iguana</i> sp. (Marie Galante) | | x | |
| <i>Leiocephalus cuneus</i> (Antigua, Barbuda) | | | x |
| <i>Leiocephalus</i> cf. <i>cuneus</i> (An- guilla, Guadeloupe) | | | x |
| <i>Leiocephalus herminieri</i> * (Martinique) | x | | |
| <i>Ameiva cineracea</i> (Guade- loupe) | x | | |
| <i>Ameiva major</i> * (Martinique) | x | | |
| <i>Boa constrictor</i> (Antigua) | | x | |
| <i>Boidae</i> sp. (Antigua) | | | x |
| <i>Alsophis</i> sp. (Barbuda) | | x | |
| cf. <i>Clelia clelia</i> (Barbuda) | | x | |

¹ Pregill et al., 1988.

context. Specifically these are the various populations of *Leiocephalus* (cf. *L. cuneus*) that occurred on Anguilla, Barbuda, Antigua, and Guadeloupe (Watters et al., 1984; Watters, 1989; Pregill, 1992). Other species of *Leiocephalus* persist on small islands in the West Indies, especially in the Bahamas, and have tolerated human settlement without obvious adverse consequences (Olson et al., 1990). For unknown reasons, the Lesser Antillean populations of *Leiocephalus* were more vulnerable.

The vertebrate fossil record for the Lesser Antilles includes a diverse list of species and genera that do not occur south or west of the Puerto Rican Bank today. The extinction of these taxa was concentrated in the Leeward Islands. From Barbuda there is a probable species of the Rock Iguana *Cyclura*, whose nearest congener is the relict *C. pinguis* of Anegada Island in the British Virgin Islands (Pregill, 1981). The Puerto Rican Parrot *Amazona vittata* survives in very small numbers in Puerto Rico's Luquillo forest and is regarded as endemic to that island. Its

occurrence in archaeological deposits on Antigua now requires a reassessment of its natural distribution. Indeed, because Amerindians may have transported parrots between islands, the natural distribution of all West Indian psittacids (*Ara* spp., *Amazona* spp., *Aratinga* spp.) is questionable in the absence of prehuman fossil evidence. The large, extinct corvid (crow, raven) from Barbuda, *Corvus* new sp., is the first Lesser Antillean record of a genus that occurs throughout the Greater Antilles. The leaf-chinned bat *Mormoops blainvillei*, which ranges throughout the Greater Antilles, is represented by fossils from Antigua and Anguilla. The big-eared bat, *Macrotus waterhousii*, occurs today no farther east than Hispaniola, but is represented by fossils from Anguilla, St. Martin, and Puerto Rico. Another species of bat, *Phyllonycteris major*, was previously known only by fossils from Puerto Rico (Koopman and Williams, 1951) until specimens were found at Burma Quarry, Antigua (Steadman et al., 1984a).

The presence of these extinct populations south

of the Anegada Passage adds context to those few extant and other recently extinct species whose congeners are likewise Greater Antillean. In this light, such Lesser Antillean outliers as the diploglossine lizard *Diploglossus montisserrati* (on Montserrat); the curly-tailed lizards *Leiocephalus* (*cuneus*, *herminieri*); the "endemic" Guadeloupe Woodpecker (*Melanerpes herminieri*); the Red-legged Thrush (*Turdus plumbeus*) on Dominica; the Rufous-throated Solitaire (*Myadestes genibarbis*) on Dominica, Martinique, St. Lucia, and St. Vincent; or Adelaide's Warbler (*Dendroica adelaide*) on Barbuda and St. Lucia appear less as distributional anomalies and more as relics of a Greater Antillean land vertebrate fauna that previously extended south and east to the Guadeloupe Passage or beyond. As is often the case with island species, their modern distribution is checkered not because of recent dispersal events, but because of extinctions on intervening islands.

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APPENDIX I—Continued

[illegible]

APPENDIX I—Continued

[illegible]

| | Somb | Angu | St.M | Saba | St.E | St.K | Nevs | Barb | Antg | Mrat | Guad | M.Gl | Mart | St.L | Gren | Bdos |
|---|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| <i>Margarops fuscus</i> Scaly-breasted Thrasher | | | | | | | | nc | | c | | | | | | |
| <i>M. fuscatus</i> Pearly-eyed Thrasher | | nc | | | c | | | nc | c/nc | c | | | | | | |
| <i>Cinclocerthia ruficauda</i> Brown Trembler | | | | | c | | | nc | nc | c | | | | | | |
| <i>Cichlherminia lherminieri</i> Forest Thrush | | | | | | | | nc | | | | | | | | |
| Turdidae sp. Thrush | | | | | | c | | | | | | | | | | |
| <i>Vireo altiloquus</i> Black-whiskered Vireo | | | | | | | | nc | | | | | | | | |
| Icteridae sp. Blackbird | | | | | | c | | | | | | | | | | |
| <i>Loxigilla portoricensis</i> cf. <i>grandis</i> "St. Kitts" Puerto Rican Bullfinch | | | | | | | | nc | | | | | | | | |
| <i>Loxigilla noctis</i> Lesser Antillean Bullfinch | | | | | | | | nc | nc | | | | | | | |
| <i>Tiaris bicolor</i> Black-faced Grassquit | | nc | | | | | | nc | | | | | | | | |
| <i>Ammodramus savannarum</i> Grasshopper Sparrow | | | | | | | | nc | | | | | | | | |
| Passeriformes sp. Passerine | | | | | c | | | | c/nc | c | | | | | | |
| Aves sp. Bird | | | | c | | c | | | nc | | | | | c | | |
| Mammals | | | | | | | | | | | | | | | | |
| <i>Didelphis marsupialis</i> Opossum | | | | | | | | | | | | | | c | c | |
| <i>Dasybus novemcinctus</i> Nine-banded armadillo | | | | | | | | | | | | | | | c | |
| <i>Pteronotus parnellii</i> Moustache bat | | | | | | | | | nc | | | | | | | |
| <i>Mormoops blainvillei</i> Leaf-chinned bat | | nc? | | | | | | | nc | | | | | | | |
| <i>Monophyllus/Glossophaga</i> Long-tongued bat? | | | | | | | | | nc | | | | | | | |
| <i>Brachyphylla cavernarum</i> Antillean fruit-eating bat | | | | | | | | | c/nc | c | | | | | | |
| <i>Phyllonycteris</i> cf. <i>P. major</i> Extinct bat | | | | | | | | | nc | | | | | | | |
| <i>Macrotus waterhousii</i> Mexican big-eared bat | | nc? | nc? | | | | | | | | | | | | | |
| <i>Natalus stramineus</i> Funnel-eared bat | | | | | | | | | nc | | | | | | | |
| <i>Tadarida brasiliensis</i> Brazilian free-tailed bat | | | | | | | | | nc | | | | | | | |
| <i>Molossus molossus</i> Velvety free-tailed bat | | | | | | | | | nc | | | | | | | |
| Chiroptera sp. Bat | | | | | c | | | | | | nc | | | | | |
| <i>Homo sapiens</i> Human | | | | | c | | | c | | c | | | | | c | |
| <i>Canis familiaris</i> Dog | | | | | c | c | | | | c | | | | c | c | c |
| <i>Dasyprocta</i> sp. Agouti | | | | | c | c | | | c | c | | c | c | | c | |

APPENDIX I—Continued

| | Somb | Angu | St.M | Saba | St.E | St.K | Nevs | Barb | Antg | Mrat | Guad | M.GI | Mart | St.L | Gren | Bdos |
|------------------------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| <i>Cavia porcellus</i> | | | | | | | | | c | | | | | | | |
| Guinea pig | | | | | | | | | | | | | | | | |
| <i>Amblyrhiza inundata</i> | | nc | nc | | | | | | | | | | | | | |
| Amblyrhiza | | | | | | | | | | | | | | | | |
| <i>Megalomys audreyae</i> | | | | | | | | nc | | | | | | | | |
| Barbuda rice rat | | | | | | | | | | | | | | | | |
| <i>Megalomys desmaresti</i> | | | | | | | | | | | | | c | | | |
| Martinique rice rat | | | | | | | | | | | | | | | | |
| <i>Megalomys luciae</i> | | | | | | | | | | | | | | | c | |
| St. Lucia rice rat | | | | | | | | | | | | | | | | |
| Oryzomyini spp. | | nc | c | | c | c | | c/nc | c/nc | c | c | c | | | c | c/nc |
| Rice rat | | | | | | | | | | | | | | | | |
| <i>Rattus</i> cf. <i>R. rattus</i> | | | | | | | | nc | c | | | | | | | |
| Black rat | | | | | | | | | | | | | | | | |
| <i>Monachus tropicalis</i> | | | | | c | | | | | | | | | | | |
| Monk seal | | | | | | | | | | | | | | | | |
| Delphinidae sp. | | | | | | | | | | | | | | | | nc |
| Porpoise | | | | | | | | | | | | | | | | |
| Cetacea sp. | | | | | c | | | | | | | | | | | |
| Porpoise/whale | | | | | | | | | | | | | | | | |
| <i>Trichechus manatus</i> | | | | | | cf | | c | c | | | | | cf | | |
| Manatee | | | | | | | | | | | | | | | | |
| <i>Bos taurus</i> | | | | | | | | | c | | | | | c | | |
| Cow | | | | | | | | | | | | | | | | |
| <i>Sus scrofa</i> | | | | | | c | | | | | | | c | | | c |
| Pig | | | | | | | | | | | | | | | | |
| <i>Capra hircus</i> | | | | | | | | c | | | | | | | | |
| Goat | | | | | | | | | | | | | | | | |
| Caprini sp. | | | | | | | | | | | | | | | | c |
| Goat/sheep | | | | | | | | | | | | | | | | |

APPENDIX II

Summary of occurrences of vertebrate remains from cultural (c) and noncultural (nc) sites in the Lesser Antilles (by island north to south). Status codes are as follows: 1 = species extant; 2 = species extinct on island, no historic record; 3 = species extinct on island, historic record exists; 4 = species extinct; 5 = introduced species. Status of birds derives from Bond (1980), Evans (1990), and our field and museum research. ? = Status uncertain.

| Taxon | Status | Context | Reference |
|--|--------|---------|---|
| SOMBRERO | | | |
| Reptiles | | | Leidy, 1868; Williams, 1952; Auffenberg, 1967 |
| <i>Geochelone sombreroensis</i> | 4 | nc | |
| ANGUILLA | | | |
| Reptiles | | | This paper |
| <i>Thecadactylus rapicauda</i> | 1 | nc | |
| <i>Sphaerodactylus</i> sp. | 1 | nc | |
| <i>Anolis</i> spp. | 1, 3 | nc | |
| <i>Leiocephalus</i> cf. <i>L. cuneus</i> | 4 | nc | |
| <i>Ameiva plei</i> | 1 | nc | |
| <i>Alsophis rijersmai</i> | 1 | nc | |

APPENDIX II—*Continued*

| Taxon | Status | Context | Reference |
|---|--------|---------|---|
| Birds | | | |
| | | | This paper; Watters, 1991 |
| <i>Puffinus lherminieri</i> | 2 | nc | |
| <i>Falco sparverius</i> | 1 | nc | |
| cf. <i>Himantopus himantopus</i> | 1 | c | |
| <i>Zenaida aurita</i> | 1 | nc | |
| <i>Columbina passerina</i> | 1 | nc | |
| <i>Margarops fuscatus</i> | 1 | nc | |
| <i>Tiaris bicolor</i> | 1 | nc | |
| Mammals | | | |
| | | | Cope, 1869a, 1869b; McFarlane and MacPhee, 1989; MacPhee et al., 1990; this paper |
| <i>Mormoops blainvillii</i> | 2 | nc | |
| <i>Macrotus waterhousii</i> | 2 | nc | |
| Oryzomyini sp. | 4 | nc | |
| <i>Amblyrhiza inundata</i> | 4 | nc | |
| ST. MARTIN | | | |
| Reptiles | | | |
| | | | Haviser, 1991; this paper |
| <i>Iguana</i> sp. | 1 | nc | |
| cf. <i>Alsophis</i> sp. | 1 | c | |
| Birds | | | |
| Columbidae sp. | 1 | c | |
| Mammals | | | |
| | | | Cope, 1869a, 1869b; McFarlane and MacPhee, 1989; Haviser, 1991; this paper |
| <i>Macrotus waterhousii</i> | 2 | nc | |
| <i>Amblyrhiza inundata</i> | 4 | nc | |
| Oryzomyini sp. | 4 | c | |
| SABA | | | |
| Birds | | | |
| | | | Josselin de Jong, 1947; Hofman and Hoogland, 1991 |
| <i>Sula</i> sp. | 1 | c | |
| Aves sp. | 1 | c | |
| ST. EUSTATIUS | | | |
| Reptiles | | | |
| | | | Versteeg 1991; van der Klift, 1992 |
| <i>Eretmochelys imbricata</i> | 1 | c | |
| Gekkonidae | 1 | c | |
| <i>Anolis</i> sp. | 1 | c | |
| <i>Iguana</i> sp. | 1 | c | |
| <i>Ameiva</i> cf. <i>erythrocephala</i> | 1 | c | |
| <i>Alsophis</i> cf. <i>rufiventris</i> | 1 | c | |
| Birds | | | |
| | | | van der Klift, 1992 |
| <i>Phaethon</i> sp. | 1 | c | |
| <i>Sula</i> sp. | 1 | c | |
| <i>Fregata magnificens</i> | 1 | c | |
| <i>Nyctanassa violacea</i> | 1 | c | |
| <i>Nycticorax nycticorax</i> | 1 | c | |
| <i>Phoenicopiterus ruber</i> | 2 | c | |
| <i>Pandion haliaetus</i> | 1 | c | |
| <i>Gallinula chloropus</i> | 1 | c | |
| Rallidae sp. | 1? | c | |
| <i>Columba leucocephala</i> | 1 | c | |
| <i>C. squamosa</i> | 1 | c | |
| <i>Geotrygon montana</i> | 2 | c | |
| cf. <i>G. mystacea</i> | 1 | c | |
| <i>Zenaida aurita</i> | 1 | c | |
| <i>Athene cunicularia</i> | 2 | c | |
| cf. <i>Margarops fuscatus</i> | 1 | c | |

APPENDIX II—Continued

| Taxon | Status | Context | Reference |
|-------------------------------------|--------|---------|---|
| cf. <i>Cinclocerthia ruficauda</i> | 1 | c | |
| Passeriformes sp. | 1 | c | |
| Mammals | | | van der Klift, 1992 |
| Chiroptera sp. | 1 | c | |
| <i>Homo sapiens</i> | 5 | c | |
| <i>Canis familiaris</i> | 5 | c | |
| <i>Dasyprocta</i> sp. | 5 | c | |
| Oryzomyini sp. | 4 | c | |
| <i>Monachus tropicalis</i> | 2 | c | |
| Cetacea sp. | 1 | c | |
| ST. KITTS | | | |
| Reptiles | | | Wing, 1973; Wing and Scudder, 1980 |
| Cheloniidae sp. | 1 | c | |
| <i>Anolis</i> sp. | 1 | c | |
| <i>Iguana delicatissima</i> | 2 | c | |
| cf. <i>Iguana</i> sp. | 1 | c | |
| <i>Ameiva</i> sp. | 1 | c | |
| cf. <i>Alsophis rufiventris</i> | 1 | c | |
| Birds | | | Hoffman, 1973; Wing and Scudder, 1980 |
| <i>Sula</i> sp. | 1 | c | |
| <i>Nyctanassa violacea</i> | 1 | c | |
| <i>Porphyryla martinica</i> | 2 | c | |
| Rallidae sp. | 1 | c | |
| <i>Larus</i> sp. | 1 | c | |
| <i>Columba</i> sp. | 1 | c | |
| Turdidae sp. | 1 | c | |
| Icteridae sp. | 1 | c | |
| Aves sp. | — | c | |
| Mammals | | | Wing, 1973; Wing and Scudder, 1980 |
| <i>Canis familiaris</i> | 5 | c | |
| <i>Dasyprocta</i> sp. | 5 | c | |
| Oryzomyini sp. | 4 | c | |
| Sirenia, cf. <i>Trichechus</i> | ? | c | |
| <i>Sus scrofa</i> | 5 | c | |
| NEVIS | | | |
| Reptiles | | | Wilson, 1989 |
| Cheloniidae sp. | 1 | c | |
| BARBUDA | | | |
| Frogs | | | Auffenberg, 1958; Lynch, 1966; Pregill et al., 1988 |
| <i>Eleutherodactylus johnstonei</i> | 1 | nc | |
| Reptiles | | | Auffenberg, 1958; Etheridge, 1964; Watters et al., 1984; this paper |
| Testudines (fam. unk.) | — | c | |
| <i>Thecadactylus rapicauda</i> | 1 | nc | |
| <i>Anolis bimaculatus</i> | 1 | nc | |
| <i>A.</i> cf. <i>A. wattsi</i> | 1 | nc | |
| <i>Leiocephalus cuneus</i> | 4 | c/nc | |
| Iguanidac (gen. and sp. unk.) | 2 | nc | |
| <i>Ameiva griswoldi</i> | 1 | c/nc | |
| <i>Alsophis</i> sp. | 2 | nc | |
| <i>Clelia</i> cf. <i>C. clelia</i> | 2 | nc | |
| Birds | | | Watters et al., 1984; this paper |
| <i>Puffinus lherminieri</i> | 2 | c/nc | |
| <i>Neochen</i> cf. <i>N. jubata</i> | 2 | nc | |

APPENDIX II—*Continued*

| Taxon | Status | Context | Reference |
|---|--------|---------|--|
| <i>Falco sparverius</i> | 1 | nc | |
| <i>Falco columbarius</i> | 1 | nc | |
| <i>Rallus limicola</i> | 2 | nc | |
| <i>Burhinus</i> cf. <i>B. bistriatus</i> | 2 | nc | |
| <i>Columba leucocephala</i> | 1 | c | |
| <i>Columba squamosa</i> | 1 | nc | |
| <i>Zenaida aurita</i> | 1 | nc | |
| <i>Columbina passerina</i> | 1 | nc | |
| <i>Geotrygon mystacea</i> | 3 | c/nc | |
| <i>Aratinga</i> new sp. | 4 | nc | |
| <i>Tyto</i> new sp. | 4 | nc | |
| <i>Athene cunicularia</i> | 2 | nc | |
| <i>Sericotes holosericeus</i> | 1 | nc | |
| <i>Orthorhynchus cristatus</i> | 1 | nc | |
| <i>Myiarchus</i> cf. <i>M. oberi</i> | 1 | nc | |
| <i>Hirundo pyrrhonota</i> | 2 | nc | |
| <i>Corvus</i> new sp. | 4 | nc | |
| <i>Mimus gundlachii</i> | 2 | nc | |
| <i>Margarops fuscus</i> | 1 | nc | |
| <i>Margarops fuscatus</i> | 1 | nc | |
| <i>Cinclocerthia ruficauda</i> | 2 | nc | |
| <i>Cichlerminia lherminieri</i> | 2 | nc | |
| <i>Vireo altiloquus</i> | 1 | nc | |
| <i>Loxigilla portoricensis</i> cf. <i>grandis</i> | 4 | nc | |
| <i>Loxigilla noctis</i> | 1 | nc | |
| <i>Tiaris bicolor</i> | 1 | nc | |
| <i>Ammodramus savannarum</i> | 2 | nc | |
| Mammals | | | Hopwood, 1926; Auffenberg, 1958; Watters et al., 1984 |
| <i>Homo sapiens</i> | 5 | c | |
| <i>Megalomys audreyae</i> | 4 | nc | |
| <i>Oryzomyini</i> new sp. | 4 | c/nc | |
| <i>Rattus</i> cf. <i>R. rattus</i> | 5 | nc | |
| <i>Trichechus manatus</i> | 2 | c | |
| <i>Capra hircus</i> | 5 | c | |
| ANTIGUA | | | |
| Frogs | | | Steadman et al., 1984a; Pregill et al., 1988 |
| <i>Eleutherodactylus johnstonei</i> | 1 | nc | |
| Reptiles | | | Wing et al., 1968; Steadman et al., 1984a; Pregill et al., 1988 |
| <i>Caretta caretta</i> | 1 | c | |
| <i>Thecadactylus rapicauda</i> | 1 | nc | |
| <i>Anolis bimaculatus</i> | 1 | nc | |
| <i>Anolis</i> cf. <i>A. wattsi</i> | 1 | nc | |
| <i>Iguana delicatissima</i> | 1 | c | |
| <i>Leiocephalus cuneus</i> | 4 | nc | |
| <i>Ameiva griswoldi</i> | 3 | c/nc | |
| <i>Typhlops monastus</i> | 1 | nc | |
| <i>Boa constrictor</i> | 2 | c | |
| cf. <i>Boidae</i> | 2 | nc | |
| <i>Alsophis</i> cf. <i>A. antillensis</i> | 3 | c/nc | |
| Birds | | | Wing et al., 1968; Steadman et al., 1984a; Pregill et al., 1988; S. L. Olson, personal communication; this paper |
| <i>Puffinus lherminieri</i> | 2 | c/nc | |
| <i>Puffinus puffinus</i> | 2 | c | |

APPENDIX II—*Continued*

| Taxon | Status | Context | Reference |
|---|--------|---------|---|
| <i>Phaethon aethereus</i> | 1 | c | |
| <i>Phaethon lepturus</i> | 1 | c | |
| <i>Sula</i> sp. | 1 | c | |
| <i>Fregata magnificens</i> | 1 | c | |
| <i>Ardeola striata</i> | 1 | c | |
| <i>Egretta</i> sp. | 1 | c | |
| <i>Nyctanassa violacea</i> | 1 | c | |
| cf. <i>Nycticorax nycticorax</i> | 1 | c | |
| <i>Phoenicopterus ruber</i> | 2 | c | |
| <i>Anas bahamensis</i> | 1 | c | |
| <i>Buteo platypterus</i> | 1 | c | |
| <i>Pandion haliaetus</i> | 1 | c | |
| <i>Poliolimnas flaviventer</i> | 2 | nc | |
| <i>Porphyryla martinica</i> | 2 | c | |
| <i>Haematopus palliatus</i> | 1 | c | |
| <i>Calidris melanotos</i> | 1 | c | |
| <i>Calidris</i> sp. | 1 | nc | |
| <i>Larus atricilla</i> | 1 | c | |
| <i>Columba squamosa</i> | 1 | c | |
| <i>Zenaida aurita</i> | 1 | c/nc | |
| <i>Columbina passerina</i> | 1 | c/nc | |
| <i>Geotrygon mystacea</i> | 1 | c | |
| <i>Amazona vittata</i> | 2 | c | |
| <i>Athene cunicularia</i> | 3 | c/nc | |
| <i>Chordeiles gundlachii</i> | 1 | c | |
| <i>Orthorhynchus cristatus</i> | 1 | nc | |
| cf. <i>Tyrannus dominicensis</i> | 1 | nc | |
| <i>Margarops fuscatus</i> | 1 | c/nc | |
| <i>Cinclocerthia ruficauda</i> | 2 | nc | |
| <i>Loxigilla noctis</i> | 1 | nc | |
| Passeriformes sp. | — | c/nc | |
| Mammals | | | Wing et al., 1968; Steadman et al., 1984a; Pregill et al., 1988 |
| <i>Pteronotus parnellii</i> | 2 | nc | |
| <i>Mormoops blainvillei</i> | 2 | nc | |
| <i>Monophyllus/Glossophaga</i> | 1/2 | nc | |
| <i>Brachyphylla cavernarum</i> | 1 | c/nc | |
| <i>Phyllonycteris</i> cf. <i>P. major</i> | 4 | nc | |
| <i>Natalus stramineus</i> | 1 | nc | |
| <i>Tadarida brasiliensis</i> | 1 | nc | |
| <i>Molossus molossus</i> | 1 | nc | |
| <i>Dasyprocta</i> sp. | 5 | c | |
| <i>Cavia porcellus</i> | 5 | c | |
| <i>Oryzomyini</i> sp. | 4 | c/nc | |
| <i>Rattus</i> cf. <i>R. rattus</i> | 5 | c | |
| <i>Trichechus manatus</i> | 2 | c | |
| Bovidae sp. | 5 | c | |
| MONTSERRAT | | | |
| Reptiles | | | Steadman et al., 1984b |
| Cheloniidae sp. | 1 | c | |
| <i>Iguana</i> sp. | 1 | c | |
| Birds | | | Steadman et al., 1984b |
| <i>Gallinula chloropus</i> | 1 | c | |
| <i>Columba squamosa</i> | 1 | c | |
| <i>Zenaida aurita</i> | 1 | c | |
| <i>Columbina passerina</i> | 1 | c | |

APPENDIX II—*Continued*

| Taxon | Status | Context | Reference |
|--|--------|---------|--|
| <i>Geotrygon mystacea</i> | 1 | c | |
| <i>Margarops fuscus</i> | 1 | c | |
| <i>Margarops fuscatus</i> | 1 | c | |
| <i>Cinclocerthia ruficauda</i> | 1 | c | |
| Passeriformes sp. | — | c | |
| Mammals | | | Steadman et al., 1984b |
| <i>Brachyphylla cavernarum</i> | 1 | c | |
| <i>Homo sapiens</i> | 5 | c | |
| <i>Canis familiaris</i> | 5 | c | |
| <i>Dasyprocta</i> sp. | 5 | c | |
| Oryzomyini new sp. A | 4 | c | |
| Oryzomyini new sp. B | 4 | c | |
| cf. Oryzomyini (large) | 4 | c | |
| cf. Oryzomyini (small) | 4 | c | |
| GUADELOUPE | | | |
| Frogs | | | This paper |
| <i>Eleutherodactylus</i> cf. <i>E. martinicensis</i> | 1 | nc | |
| <i>Bufo marinus</i> | 5 | nc | |
| Reptiles | | | Barbotin, 1970; Pregill, 1992; this paper |
| <i>Hemidactylus</i> cf. <i>H. mabouia</i> | 1 | nc | |
| <i>Thecadactylus rapicauda</i> | 1 | nc | |
| <i>Anolis marmoratus</i> | 1 | nc | |
| <i>Iguana</i> sp. | 1 | c/nc | |
| <i>Leiocephalus</i> cf. <i>L. cuneus</i> | 4 | nc | |
| <i>Ameiyya</i> cf. <i>A. cinceracea</i> | 3 | nc | |
| <i>Typhlops</i> cf. <i>T. dominicana</i> | 1 | nc | |
| cf. <i>Alsophis antillensis</i> | 1 | nc | |
| Mammals | | | Wing et al., 1968; Barbotin, 1970; this paper |
| Chiroptera spp. | — | nc | |
| Oryzomyini sp. | 4 | c | |
| MARIE GALANTE | | | |
| Reptiles | | | Barbotin, 1970; Wing, 1973 |
| Cheloniidae sp. | — | c | |
| cf. <i>Iguana</i> | 2 | c | |
| Birds | | | Wing, 1973 |
| <i>Columba</i> sp. | 1 | c | |
| <i>Zenaida</i> sp. | 1 | c | |
| Mammals | | | Barbotin, 1970; Wing, 1973 |
| <i>Dasyprocta</i> sp. | 5 | c | |
| Oryzomyini sp. | 4 | c | |
| <i>Sus scrofa</i> | 5 | c | |
| MARTINIQUE | | | |
| Reptiles | | | Hoffstetter, 1946; Allaire, 1977; Fraser, 1981 |
| <i>Caretta caretta</i> | 1 | c | |
| <i>Eretmochelys imbricata</i> | 1 | c | |
| <i>Lepidochelys</i> sp. | 1 | c | |
| Cheloniidae sp. | 1 | c | |
| <i>Iguana</i> sp. | 1 | c | |
| Birds | | | Wetmore, 1952; Allaire, 1977; Fraser, 1981 |
| <i>Pterodroma hasitata</i> | 2 | c | |
| <i>Buteo platypterus</i> | 1 | c | |
| <i>Porphyryula martinica</i> | 2 | c | |
| <i>Limnodromus griseus</i> | 1 | c | |
| <i>Columba squamosa</i> | 1 | c | |
| <i>Zenaida aurita</i> | 1 | c | |

APPENDIX II—Continued

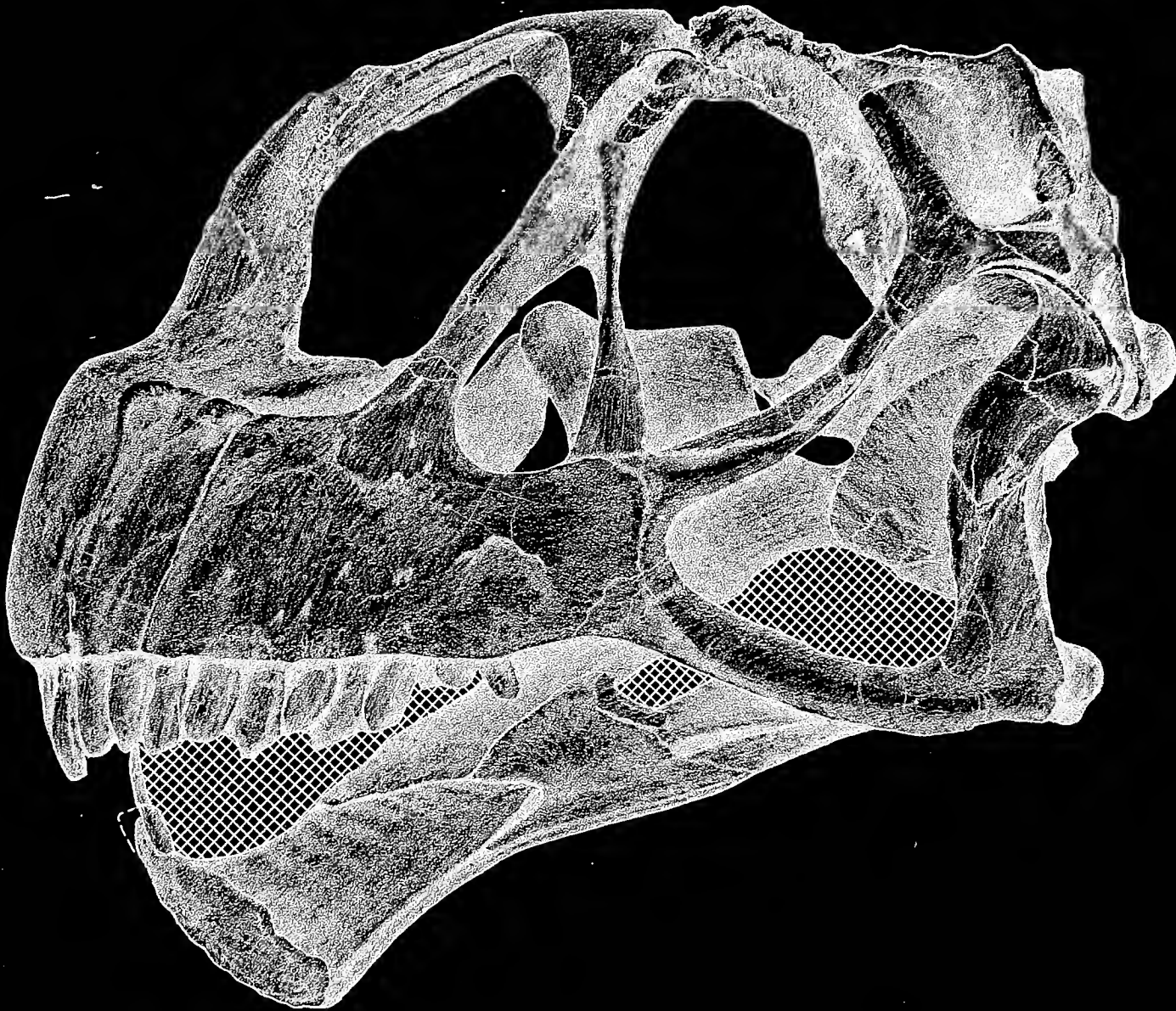
| Taxon | Status | Context | Reference |
|--|--------|---------|---|
| Mammals | | | Friant, 1941; Allaire, 1977; Fraser, 1981 |
| <i>Dasyprocta</i> sp. | 5 | c | |
| <i>Megalomys desmarestii</i> | 3 | c | |
| <i>Trichechus</i> sp. | 2 | c | |
| <i>Bos taurus</i> | 5 | c | |
| ST. LUCIA | | | |
| Reptiles | | | Wing, 1968 |
| Cheloniidae sp. | 1 | c | |
| <i>Iguana</i> sp. | 1 | c | |
| Birds | | | Wing, 1968 |
| Aves sp. | 1 | c | |
| Mammals | | | Wing, 1968 |
| <i>Didelphis marsupialis</i> | 5 | c | |
| <i>Canis familiaris</i> | 1 | c | |
| <i>Megalomys luciae</i> | 3 | c | |
| GRENADA | | | |
| Reptiles | | | Bullen, 1964; Fandrich, 1990 |
| <i>Chelonia mydas</i> | 1 | c | |
| <i>Lepidochelys</i> cf. <i>L. olivacea</i> | 1 | c | |
| <i>Iguana</i> sp. | 1 | c | |
| Birds | | | Fandrich, 1990 |
| <i>Puffinus lherminieri</i> | 1 | c | |
| <i>Pelecanus occidentalis</i> | 1 | c | |
| <i>Pandion haliaetus</i> | 1 | c | |
| Mammals | | | Bullen, 1964; Lippold, 1991; Fandrich, 1990 |
| <i>Didelphis marsupialis</i> | 5 | c | |
| <i>Dasypus novemcinctus</i> | 5 | c | |
| <i>Homo sapiens</i> | 5 | c | |
| <i>Canis familiaris</i> | 5 | c | |
| <i>Dasyprocta</i> sp. | 5 | c | |
| Oryzomyini sp. | 4 | c | |
| BARBADOS | | | |
| Reptiles | | | Swinton, 1937; Ray, 1964a; Wing, 1991 |
| <i>Chelonia mydas</i> | 1 | c | |
| <i>Geochelone</i> sp. | 4 | nc | |
| <i>Anolis (roquet) extremus</i> | 1 | nc | |
| <i>Iguana iguana</i> | 2 | nc | |
| <i>Liophis perfuscus</i> | 1 | nc | |
| Colubridae sp. | 1 | c | |
| Birds | | | Brodkorb, 1964; Wing, 1991 |
| <i>Puffinus lherminieri</i> | 1 | nc | |
| <i>Dendrocygna arborea</i> | 3 | nc | |
| <i>D. autumnalis</i> | 3 | nc | |
| <i>Dendrocygna</i> sp. | 3 | c | |
| <i>Neochen</i> cf. <i>N. jubata</i> | 4 | nc | |
| <i>Aythya collaris</i> | 1 | c | |
| <i>Buteo jamaicensis</i> | 3 | nc | |
| <i>Gallus gallus</i> | 5 | c | |
| <i>Porphyryula martinica</i> | 3 | c | |
| <i>Fulica podagrica</i> | 4 | nc | |
| Columbidae sp. | 1 | c | |
| <i>Mimus</i> sp. | 2/4 | c | |
| Mammals | | | Ray, 1964a; Wing, 1991 |
| <i>Canis familiaris</i> | 5 | c | |
| Oryzomyini new sp. | 4 | c/nc | |

APPENDIX II—*Continued*

| Taxon | Status | Context | Reference |
|-------------------|--------|---------|-----------|
| Delphinidae sp. | 1 | nc | |
| <i>Sus scrofa</i> | 5 | c | |
| Caprini sp. | 5 | c | |

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SKULL AND ATLAS-AXIS COMPLEX OF THE
UPPER JURASSIC SAUROPOD
CAMARASAURUS COPE (REPTILIA: SAURISCHIA)

JAMES H. MADSEN, JR., JOHN S. McINTOSH, AND DAVID S. BERMAN

